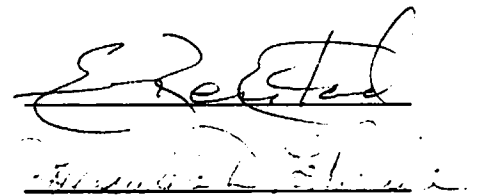


HETEROGENEITY AND BIAS IN ABUNDANCE ESTIMATES OF
OUTMIGRATING CHINOOK SALMON IN THE CHENA RIVER,
ALASKA

By

Theodore Martelle Lambert

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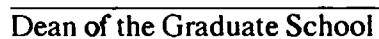

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**Heterogeneity and Bias in Abundance Estimates of
Outmigrating Chinook Salmon in the Chena River, Alaska**

A Thesis
for the Degree of
Master of Science

by
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Abstract

The objective was to examine bias due to heterogeneity in capture probability (p) in an abundance estimate for chinook salmon (*Oncorhynchus tshawytscha*) outmigrants in the Chena River, Alaska. A higher proportion of day-marked fish ($21 / 636 = 0.0330$) compared to night-marked fish ($17 / 1724 = 0.0098$; $p < 0.0001$, $\alpha = 0.05$) was recaptured at the lower site in a Cormack-Jolly-Seber experiment with upper, middle and lower sites. Heterogeneity was also likely at the middle site between upper site-marked and unmarked fish. Simulations with heterogeneity confined to the middle and lower sites (i.e., due to inadequate mixing) caused small bias ($< 2.5\%$) in the upper site abundance estimate. With heterogeneity at all three sites (a subpopulation effect), the upper site estimate had 22.9% to 29.3% negative bias. Because heterogeneity observed in the Chena was probably due to inadequate mixing (related to daytime trap evasion), bias in the upper site estimate was probably small.

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Introduction

Background

This study was part of a larger investigation of the effects of the Chena River Flood Control Project on outmigrating chinook salmon (*Oncorhynchus tshawytscha*) and chum salmon (*Oncorhynchus keta*) in the Chena River, Alaska. The flood control project includes an 11.3 km diversion dam which partially diverts floodwater from the Chena through a cleared floodway and into the Tanana River, bypassing Fairbanks (Figure 1). The gates are lowered only during flood events, with the objective of maintaining a maximum flow of 12,000 cfs through downtown Fairbanks.

Since the dam was completed in 1973, the three largest flood control events were in 1985, 1991, and 1992, all during the spring break-up period (May to early June) when juvenile chum and chinook salmon begin downstream migration to the Bering Sea via the Yukon River drainage. Chum salmon outmigrate soon after hatching, at age-0, during peak flow associated with spring breakup. Chinook salmon outmigrate as age-1 or age-2 juveniles over a longer period, but primarily May and June.

Public concern was expressed that control events during spring could affect these outmigrants through delay and, ultimately, increased mortality due to entrapment in the floodway or physical damage due to the dam hydraulics. During 1981-1983, the U.S. Fish and Wildlife Service documented the timing and duration of outmigration just downstream of the floodgates, but this study was not designed to evaluate the effects of project operation on outmigration or abundance.

In 1994 the U.S. Army Corps of Engineers funded the present study, to be carried out by the Alaska Cooperative Fish and Wildlife Research Unit. The three objectives of the

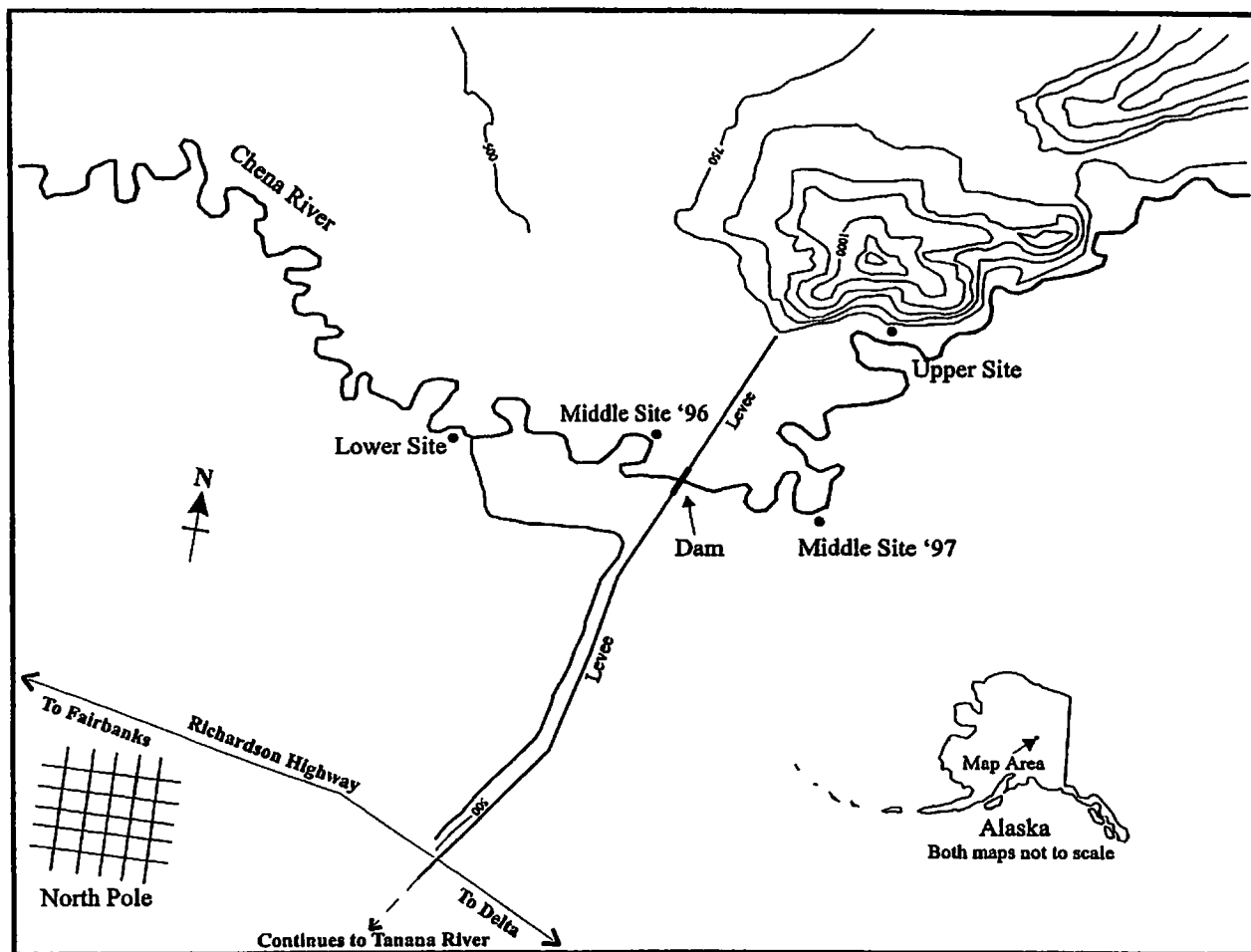


Figure 1. Map of the Chena Lakes study area. The upper and lower sites were the same in 1996 and 1997.

study were to: estimate the movement, abundance and survival of outmigrants in event and non-event years; compare the condition of outmigrants upstream and downstream of the dam in both event and non-event years; and to evaluate the contribution of the Chena to salmon abundance in the Tanana and Yukon Rivers.

Unit students Brent Peterson and Michael Daigneault addressed objectives 1 and 2, respectively, establishing baseline estimates for the non-flood 1996 season (Peterson 1997, Daigneault 1997). Abundance and survival were estimated with mark-recapture, using three trapping sites and a Cormack-Jolly-Seber (CJS) model. Screw traps with 5 ft (168 cm) diameter cones (Figure 2) were used at the upper and lower sites and an inclined plane trap (Figure 3, Todd 1994) was used at the middle site.

This paper describes an attempt in 1997 to examine the soundness of the baseline abundance estimate for one species, chinook salmon, with regard to the CJS assumption of equal capture probability among all animals in the population. Heterogeneity in capture probability among chum salmon was not suspected (their capture rates were steady over a 24 hour period, the implications of which are discussed below), so chum salmon were not part of the heterogeneity experiment.

Heterogeneity Issue

Heterogeneity in capture probability (p) is a common cause of abundance underestimation (i.e., negative bias) in Cormack-Jolly-Seber (CJS) experiments (Cone et al. 1988; Pollock et al. 1990). In many populations, some animals are innately easier to catch than others because, for example, they are less wary or more susceptible because of living habits. This results in animals with higher p being captured and marked before more elusive animals in the population. If the capture probability of the elusive individuals in the

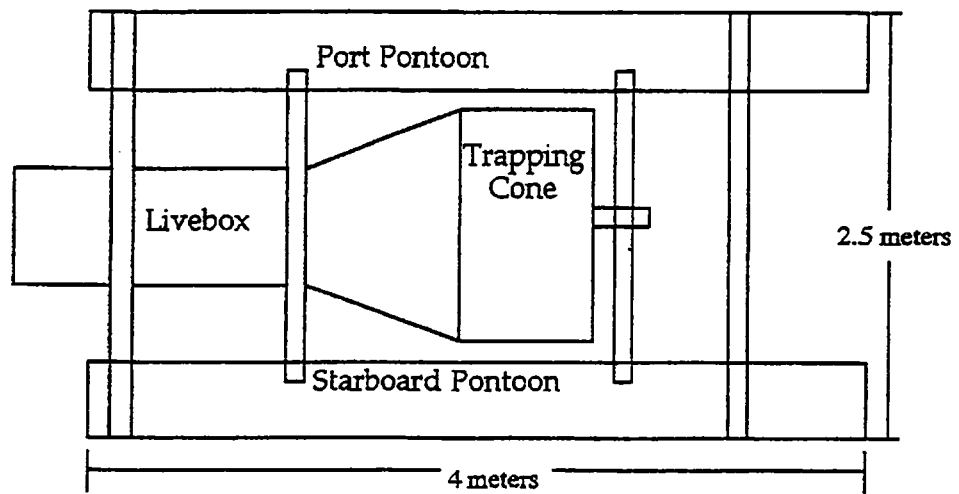


Figure 2. Diagram of a screw trap, used at the upper and lower sites.

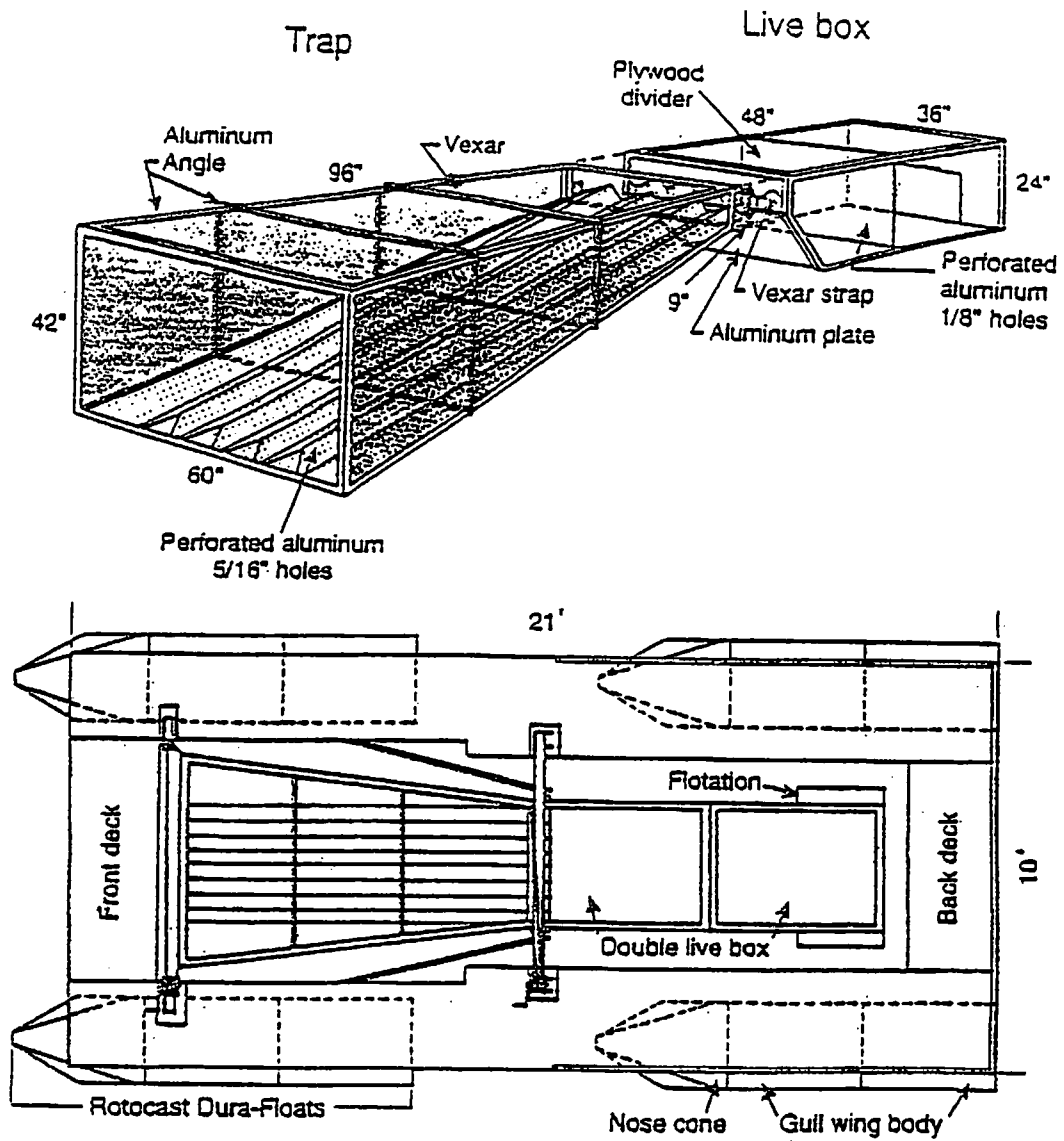


Figure 3. The inclined plane trap used at the middle site (see Todd [1994] for further description). Reprinted courtesy of Gary Todd.

population remains low in subsequent sampling periods, elusive individuals will be under-represented or perhaps totally absent from the samples, causing underestimation of population abundance (Cone et al. 1988, Gilbert 1973, Pollock et al. 1982). Concern about heterogeneity is one of the reasons for the CJS assumption that “every animal present in the population at the time of the i th sample ($i = 1, 2, \dots, k$) has the same probability of capture” (Pollock et al. 1990).

Heterogeneity in p and negative bias was considered a possibility in the baseline 1996 CJS abundance estimate for chinook salmon. Cause for suspicion was that, for unknown reasons, daytime trapping with a screw trap consistently caught very few chinook particularly at the downstream site (Figure 4; Peterson 1997). Daytime trapping was therefore abandoned. This would have little or no potential to affect the estimates if the low daytime capture rates were due to chinook not migrating during the day. All chinook would be exposed to capture as they swam past the traps at night and they would presumably (at least with respect to diel behavior) have equal capture probabilities. However, if chinook were actually migrating during the day, but were less vulnerable to capture at that time due to increased trap evasion or swimming lower in the water column and beneath the traps, heterogeneity in p could potentially exist. For example, if chinook were to migrate during the day when they were less vulnerable to capture, and some individuals in the population had a greater propensity to migrate during the day than others, a portion of the population would be relatively unsampled and negative bias would result (Pollock 1990). Heterogeneity would in this case be due to a subpopulation effect.

Decreased vulnerability of day-swimming fish would not alone cause heterogeneity. If fish were well distributed spatially by the time they reached a downstream trap, and there

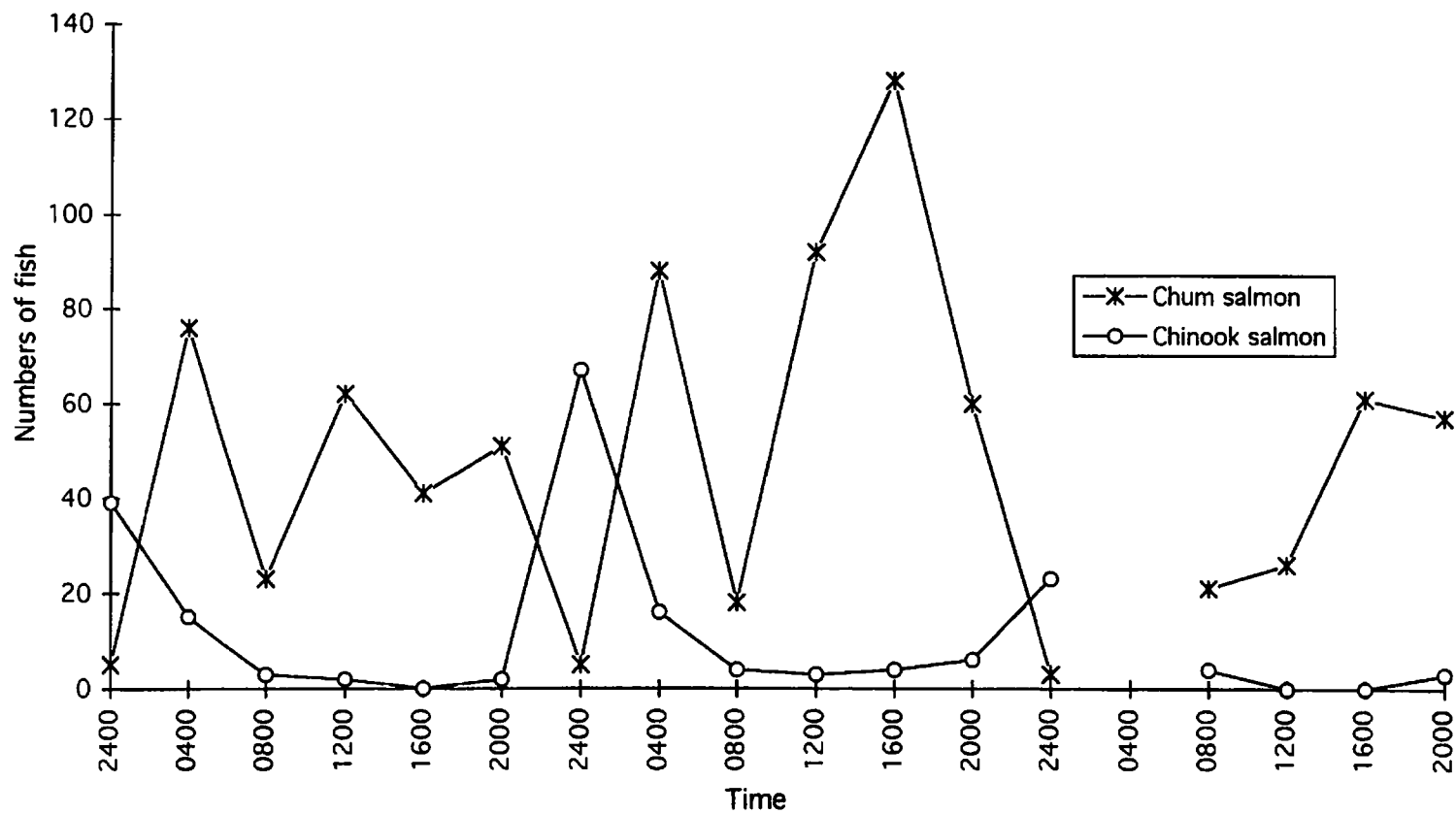


Figure 4. Diel capture rates for chinook and chum salmon at the lower site screw trap, May 10-12, 1995.

were no tendencies for subpopulations to migrate at different times, all fish, marked and unmarked, would have an equal probability of A: passing a downstream trap at night, and B: being captured during passage at night (all fish would have $p_{i+1} = A * B$ upon release on occasion i). This would be analogous to a gillnet stretching across only half a lake not necessarily causing heterogeneity, *if* the fish were well mixed between samples and no subpopulations with unequal tendencies to swim on either side of the lake existed.

Heterogeneity due to inadequate mixing could also exist, especially if outmigrants are marked for less than 24 hour periods (at night only, for example). The current could just happen to consistently deliver pulses or schools of fish originally caught at night to a downstream trap during the day, when the downstream trap was relatively ineffective. Similarly, unmarked fish, which swam under the upstream trap during the day, might consistently arrive at the downstream trap at night, and thus be over-represented in the sample. This could be called a “timing effect”. As part of a capture efficiency experiment to estimate abundance, coho salmon smolts (*Oncorhynchus kisutch*) in Deep Creek, Kenai Peninsula, Alaska, were released about 150 m upstream of the trap at 1500, and 2.4 km upstream at 1700. The trap was fished 24 hours. Fish released 150 m upstream had a recapture ratio of 0.22, while fish released 2.4 km upstream had a recapture ratio of 0.40 (David Bernard, Alaska Department of Fish and Game, personal communication). The fish marked further upstream may have tended to arrive at the trap during the night, when the trap was likely to have been more effective, accounting for the higher proportion of recaptures for fish released far upstream. This combination of migration timing and changes in diel vulnerability to the trap seems a likelier cause than short-term trap shyness. In another experiment on Deep Creek at the same location (Bendock 1996), equal numbers of chinook (≥ 100 per release at each site) were released approximately 100 feet upstream at

1500 hours and approximately 1.5 km upstream at 1700 hours on June 21 and June 28, 1995. For the June 21 release, recapture ratios were 0.42 and 0.10 for the distant and near releases, respectively, and were significantly different with $\chi^2 = 16.5$, $df = 1$, $p < 0.001$. On June 28, the ratios were 0.091 and 0.017 for the June 28 release ($\chi^2 = 5.6$, $df = 1$, $p = 0.02$). For the following five consecutive weekly releases, the downstream release was delayed until 2300 hours. With the near-release fish reaching the trap at night, none of the five pairs of recapture ratios were significantly different ($\chi^2 = 0.00 - 2.02$, $df = 1$, $P = 0.16 - 1.00$).

If chinook in the 1996 Chena River CJS experiment experienced similar changes in diel vulnerability to the traps, and fish did not become randomly dispersed in the river between sites (both spatially and among unmarked fish), heterogeneity in p could have existed at the middle and lower capture sites. Fishing the traps during the night only would have exacerbated such an effect. Therefore, the purpose of the 1997 season, in the absence of a flood event, was to test for heterogeneity in capture probability. The soundness of the 1996 estimate with respect to any detected heterogeneity would then be examined. The 1997 heterogeneity experiment was embedded in a CJS experiment similar to in the previous 1996 season; because they were intertwined, both are presented and discussed.

Methods

Notation

Cormack Jolly Seber (CJS) notation (following Pollock et al. 1990), estimators and assumptions are presented and briefly discussed in Appendix 1. Two CJS symbols frequently occurring in this text are:

ϕ_i = survival probability in interval i , and

p_i = capture probability at site (“occasion”) i .

Two symbols specific to this text, used as parameter indices, are:

d = chinook caught at the middle site during the day (between 0900 and 1700), and

n = chinook caught at the middle site during the night (between 2100 and 0500).

They are placed before the occasion index, for example, ϕ_{d2} = survival for “day” fish on the second occasion (between the middle and lower sites). Because they are used as parameter indices only, they should not be confused with the statistic n_i (sample size, defined in the Appendix 1).

Other symbols and definitions are:

ρ_i = recapture rate (rho), the number of marked fish captured in i divided by the number marked and released in $i-1$, equal to $\phi_{i-1} * p_i$,

D_i = heterogeneity in capture probability, equal to $p_{di} - p_{ni}$, and

$$\text{PRB} = \text{percent relative bias, or } \frac{N_i - \hat{N}_i}{N_i} * 100.$$

Chinook Mark-Recapture Experiment

The 1997 CJS mark-recapture experiment differed little from the 1996 experiment. The minimum of three trapping sites were distributed within the same 15.8 km stretch of the Chena River as in 1996, and had the same upper and lower sites (Figure 1). Smolts captured at the upper site were marked with a partial upper caudal fin clip. At the middle site, fish were inspected for upper fin clips and marked with a lower caudal clip. The lower site was for inspection of marks only.

The only significant departures from the 1996 CJS experiment methods occurred at the middle site, and were made to accommodate the test for heterogeneity in capture probability. Unlike the upper and lower 1997 sites, or any site in 1996, the middle site inclined plane trap was fished surface-to-bottom for both day and night periods. Additional marks (partial pelvic fin clips) distinguished day and night captures. The 1997 middle site was also located 5.4 km upstream from the 1996 site (distances are in Table 1), both to find a suitably shallow, gradually sloping streambed profile and to increase the potential for mixing of day- and night-marked fish.

Setting the upstream trap was the first priority, because marked fish require time to reach the next downstream site before the experiment could begin. The upper site screw trap was towed upstream and began fishing on May 6 at 2000; at the lower site, fishing began at 1900 on May 7. The lower site was easy to set up, being downstream of the

Table 1. River kilometers (miles) between sites in the Chena River study. A new middle site was required for the 1997 heterogeneity experiment.

	Upper	Middle (1996)	Middle (1997)	Lower
Upper	-	11.8 (7.3)	6.4 (4.0)	15.8 (9.8)
Middle (1996)	11.8 (7.3)	-	5.4 (3.3)	4.0 (2.5)
Middle (1997)	6.4 (4.0)	5.4 (3.3)	-	9.4 (5.8)
Lower	15.8 (9.8)	4.0 (2.5)	9.4 (5.8)	-

launch area and road accessible. Because a new middle site suitable for the heterogeneity experiment had to be found and setting up was more difficult, the inclined plane trap did not begin fishing until May 9 at 0900. All traps were anchored with cable or rope to trees or large (1.5 m) metal stakes, and had a safety rope tied between the rear of the trap and shore in case the main line pulled out or broke.

The upper and lower site screw traps, located on swift outside bends with steep banks, were propped into the main current with wooden gang planks about 4 m long. The planks also provided access to the traps. The middle site inclined plane trap was anchored away from the bank, requiring wading (set-up of the inclined plane trap is covered in the following section).

The upper and lower sites screw traps were, as in 1996, only fished between 2000 and 0800 hours due to limited worker hours and because the screw traps had proven inefficient during the daytime. The screw traps were emptied of fish every 3 hours for most of the season (see Appendix 2: Raw Data).

Smolts at all sites were anesthetized in a solution of MS-222 before handling (inspection and marking). Upon losing equilibrium, the fish were placed in petri dish of fresh river water while they were marked or inspected for marks. Fork length (mm) was measured, chinook were judged as smoltified (silvery) or not and, at the upper and lower sites, fish were inspected for scale-loss and injury (for comparison to condition data in case of a 1997 flood event). All fish were put in a bucket of fresh river water for recovery, and were not released until full recovery was apparent.

Throughout the season, fish were given at least 15 minutes to recover (regain equilibrium and resume respiration) before being released. Those that did not recover, or appeared sluggish, were not released. Fish usually took less than 5 minutes to recover.

During 1997 there were 41 losses on capture at the upper site and 44 at the middle site. Almost all of the upper site losses were killed or mortally wounded from the screw trap, averaging about 1 or 2 per 3-hour period in the early season when capture rates and debris loads were high (Appendix 2). Fish caught in the screw trap were usually uninjured or severely injured. Injury usually involved a severely crushed body part, either from getting caught between the junction of the cone and livebox or amongst moving debris. Only healthy fish were marked and released. The middle site inclined plane trap killed only 3 chinook. Most of the middle site losses (2 marked and 32 unmarked) occurred during an accident while working up fish caught between 2100 and 0100 of the first night (May 9). I noticed that recently marked fish in the recovery bucket of “fresh” water were not recovering as quickly as normal. After pouring them into another bucket, I found a greenish, dirt-covered residue of old dish-washing detergent from the previous year in the bottom of the bucket. After half an hour the fish never regained their equilibrium or were dead, so they were not released.

Camps were set up on May 1. Although the river was clear except for occasional chunks of drifting ice, thick (about 60 cm) ice still blocked a channel between the boat launch and the river. On May 5 we were able clear a path for the boats and traps by prying apart large pans of ice (5 to 10 m across) with steel bars.

The study had enough money to fund personnel until June 14th, requiring us to begin pulling traps out of the river on June 11. Capture rates were extremely low in the first week of June (< 10 chinook/day at all sites), suggesting (falsely, as later explained) that the main outmigration for chinook was over. The upper site trap was shut down earliest, on June 10 at 1900. Coincidentally, a spate of very quickly rising water from a rainstorm 3 days earlier hit the study area about that time (Figure 5, the June 10 measurement in the

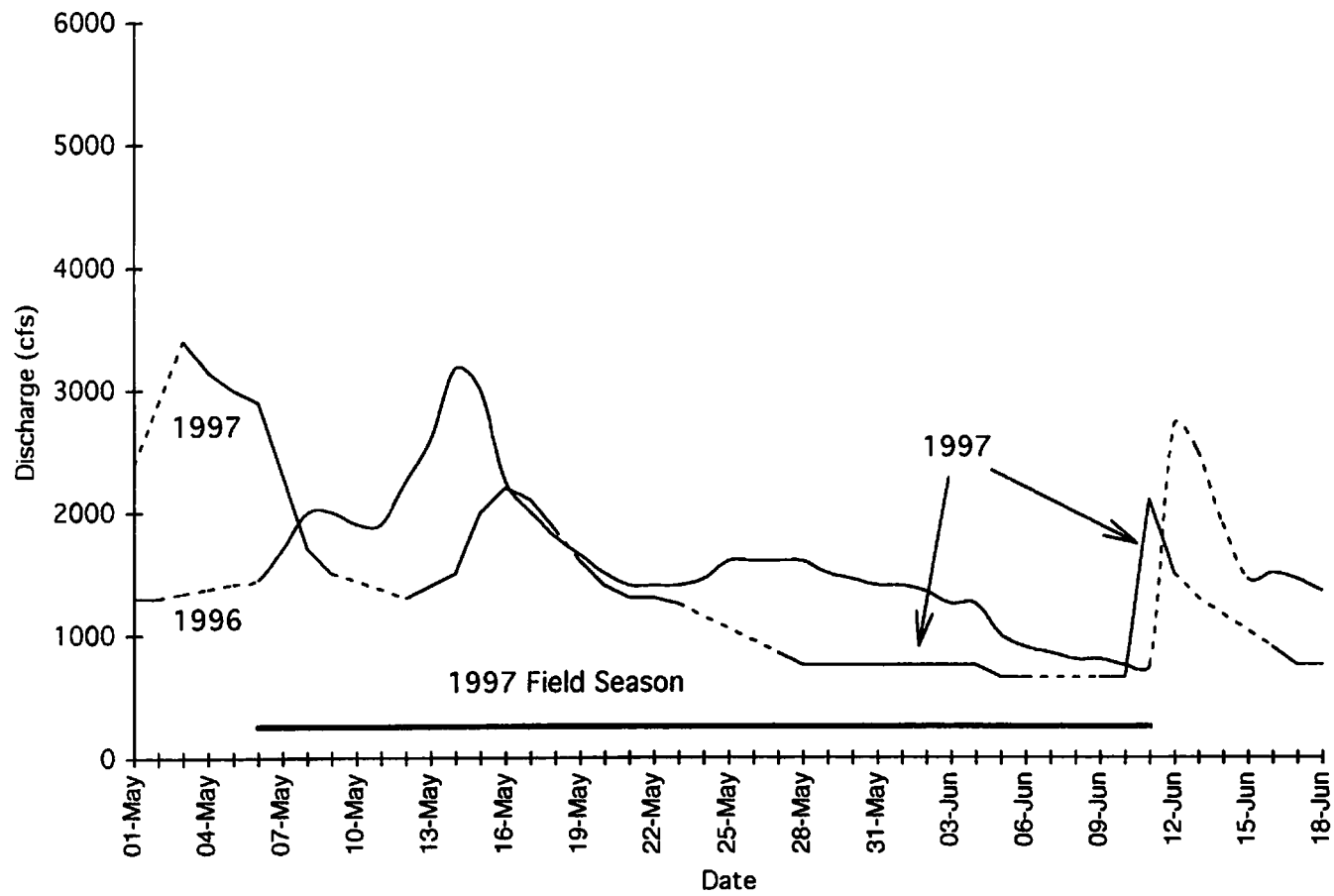


Figure 5. Discharge at the Chena River Dam in May and early June, 1996 and 1997. The dashed lines represent no data recorded.

graph was taken at 0815). Debris clogged the lower site screw trap faster than it could be removed from the trapping cone, forcing the crew to stop fishing at 0130 on June 11. The debris frequently stopped the cone from spinning, and half or more of the fish captured were dead or severely injured. Removing the debris was painstaking and dangerous. The cone had to be raised, and someone had to climb in and, in a very difficult, confined position, remove the debris by hand. An additional person was needed to steady the cone and remove debris as it was handed out. A length of 2x6 inch lumber was wedged between the bottom of the cone and the pontoons to keep the cone from falling into the water should the supporting winch or cable give way.

The middle site inclined plane trap was much easier to keep clear of debris, and was very effective during high water. During peak flow, the trap had to be cleared of sticks about every 20 to 30 minutes. However, one person could easily accomplish this without raising the plane (the trap could keep fishing).

Capture rates at the middle site were extremely high during the spate, particularly at night (Figure 6). In seven hours of actual fishing between 2100 on June 10 and 0600 on June 11, 586 chinook were captured. The total of 336 fish captured in only one hour between 2100 and 2200 was more than in any 24 hour period (16 hours of actual fishing) in the preceding season. The numbers of fish were so great that I had to boat a technician up from the lower site to help work-up the fish, so the trap was raised between 2200 and 0100. After that the trap was emptied hourly between 0100 and 0600. Catches at all sites (Figure 7) fell to negligible levels when discharge was less than 1000 cfs; at other times before and after the low-flow period, when discharge exceeded 1000 cfs, catches were higher (compare Figures 5 and 7).

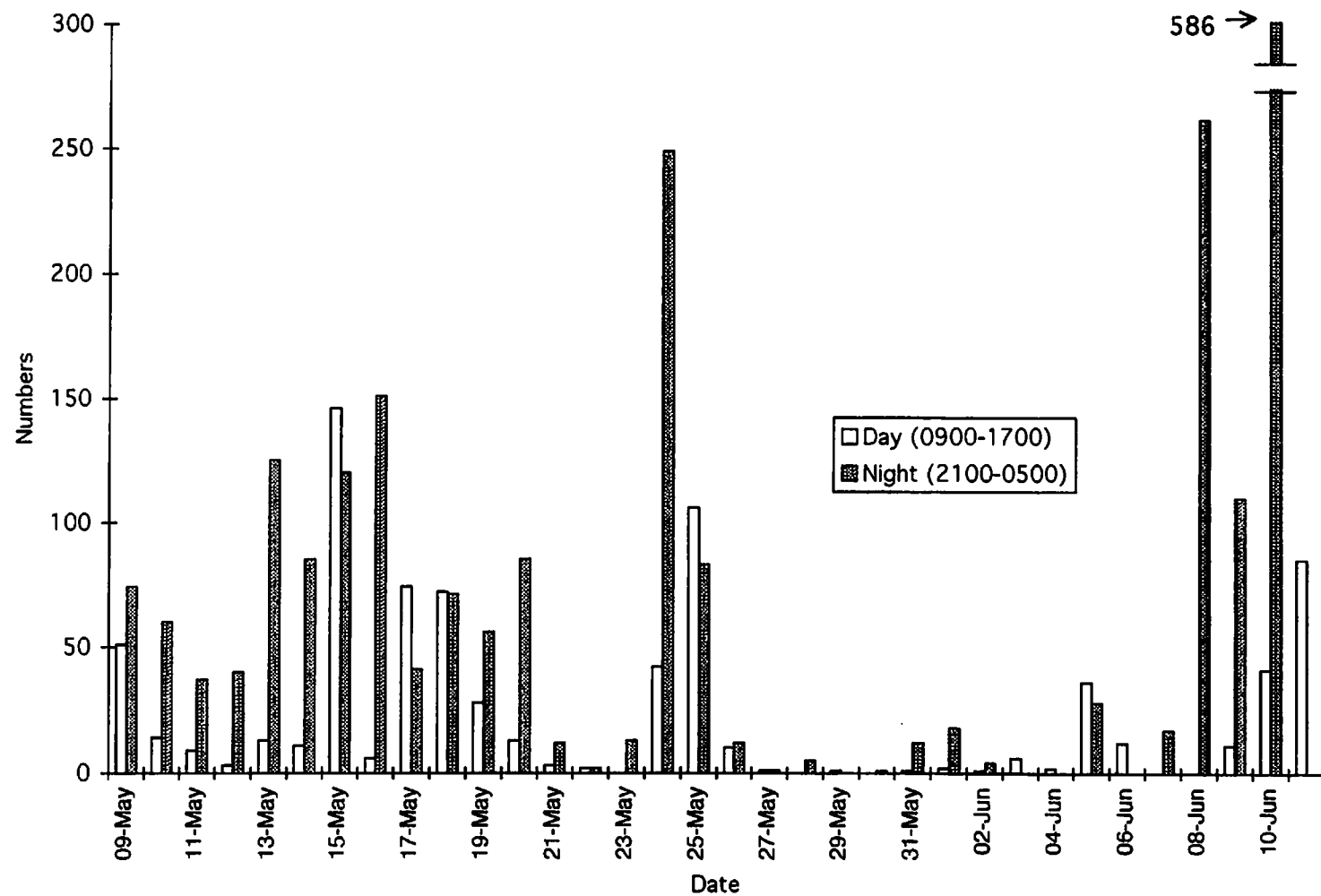


Figure 6. Numbers of chinook captured during the day and at night at the middle site, 1997.

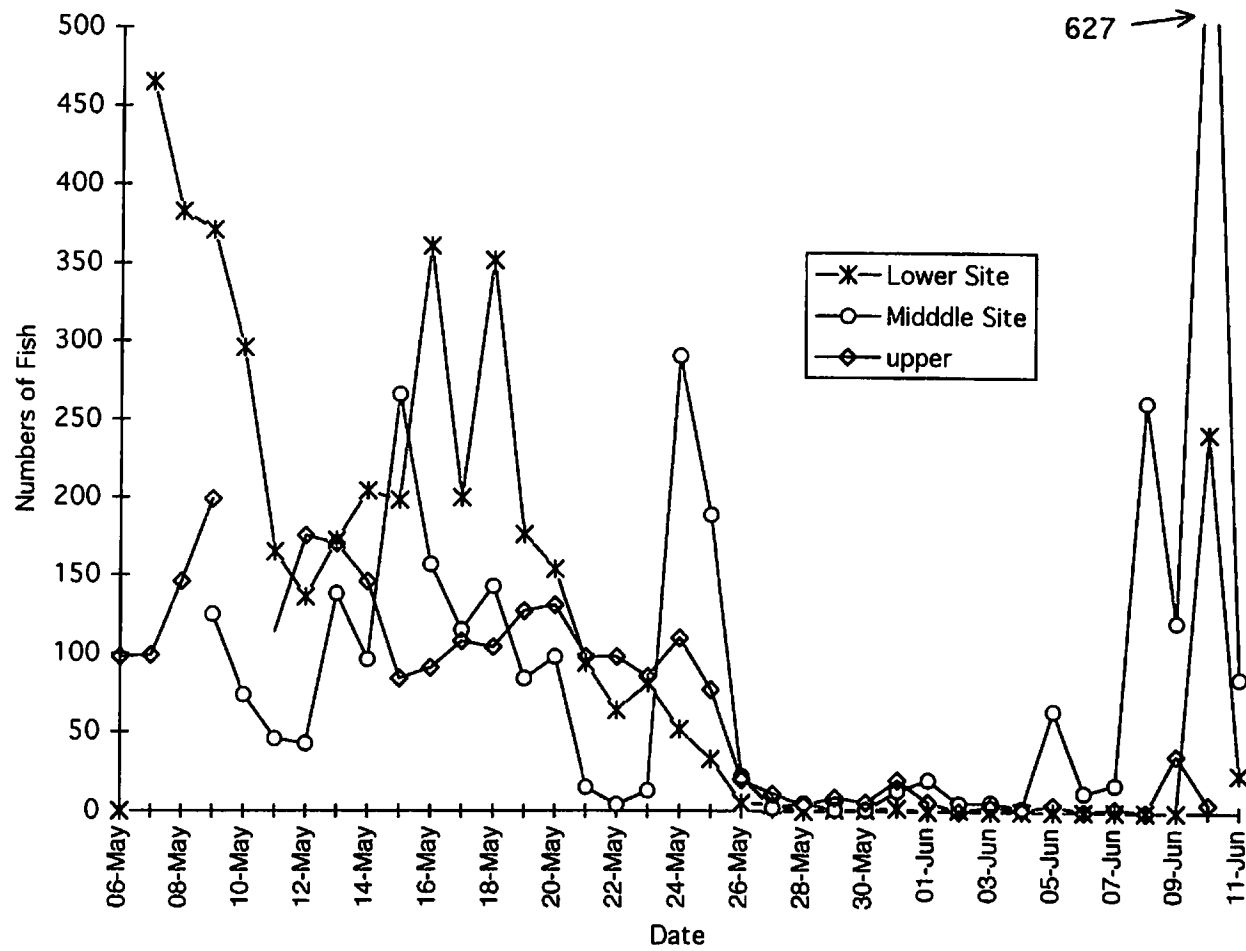


Figure 7. Total chinook catches by date at all sites, 1997.

The cut-off times for including mark-recapture data in the CJS experiment were staggered among sites to allow marked and unmarked fish to reach the lower sites. Because the lower site was for recaptures only, fish captured through the last period of fishing (1000 on June 11) were included as lower site CJS data. Allowing for at least 36 hours travel between sites, the cutoff point for middle site releases was at 0500 on June 8. However, the last period in which marked fish were recaptured at the middle site was between 0900-1700 on June 10, just before the spate hit (2 upper caudal clipped fish were caught). I therefore included fish caught in the period 0900-1700 on June 10 as captures at the middle site. Because these fish probably did not have enough time to reach the lower site before it stopped fishing at 1000 on June 11, the two marked and 39 unmarked fish caught during period between 0900 to 1700 on June 10 were counted as “losses on capture” in the middle site data. (Fish that are marked, but unavailable for recapture, are essentially losses on capture and should be accounted for in the CJS model.) Despite the extraordinarily high catch rates just hours later during the spate, no more marked fish were caught, so the cutoff time for middle site “losses on capture” was 1700 on June 10. Finally, to give upper site-marked fish time to reach the middle site before 1700 on June 10, the cutoff time for upper site releases was 0700 on June 9.

The Heterogeneity Experiment

A new upstream site was required to fish the inclined plane trap surface to bottom and prevent day-migrating chinook from swimming beneath the trap. The water had to be less than 80 cm deep, have fairly swift current, and the bottom profile had to slope gradually so the trap could be moved laterally with changing water level and still fish surface to bottom. In previous years, all trapping sites were located in swift water along

outside bends in relatively deep water. While there were suitable bottom profiles downstream of the old middle site, they were judged too close to the lower site for adequate mixing between day-release and night-release fish. Longer distances between sites would lessen the chances of confounding heterogeneity due to different subpopulations with heterogeneity due to mixing. The closest place upstream with a good profile (Figure 8) was 5.4 km upstream of the old middle site. The middle-to-lower-site distance increased from 4.0 to 9.4 kilometers.

The middle site inclined plane trap was held in position from 5 to 15 m offshore (depending on the water level) with several metal fenceposts pounded into the streambed along the shoreward trap pontoon. Cords tied between the tops of posts and the pontoon on the opposite side steadied the trap in even swift water (about 1 m/s). There was also a short bridle rope spanning the tips of the pontoons. Adjusting the point at which the main trap-to-shore rope was tied to the bridle rope (before pounding the fenceposts), and thereby the angle and distance the trap naturally planed away from shore, kept most of the pressure off of the fenceposts. The inclined plane trap was maintained in about 80 cm of water (to where the lip of the plane just touched bottom) throughout the season by moving its lateral position in the stream.

The trap was fished from 0900-1700 (*d*) and 2100-0500 (*n*). When capture rates were high, primarily in the early season, fish were removed from the trap every four hours. During times of low catch rates, the trap was emptied every eight hours (Appendix 2). The inclined plane trap was cleaned of sticks and leaves as needed, from every 2-8 h in times of low water to every 0.5 h during the end of season spate.

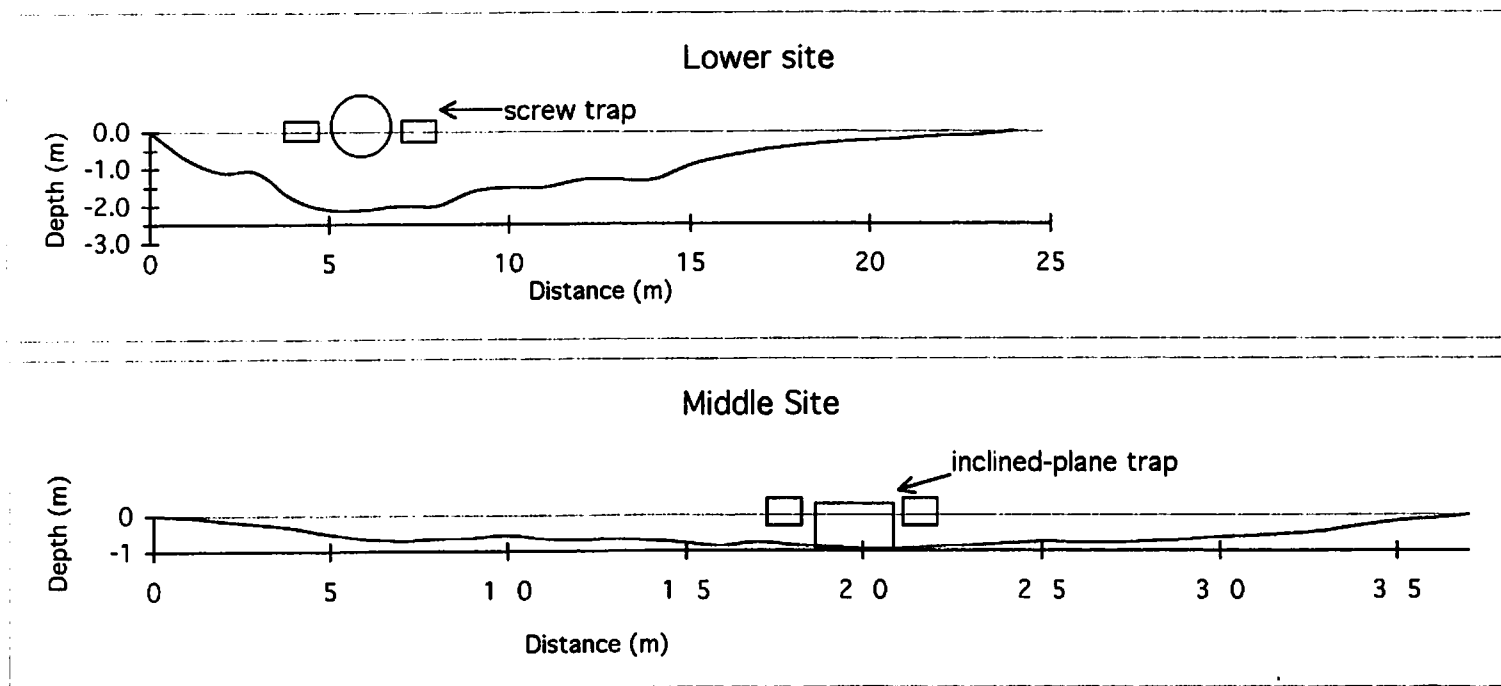


Figure 8. Depth profiles at the lower and middle sites, looking downstream, on June 7th, 1997.

Chinook caught at the middle site during the day (between 0900 and 1700, local daylight savings time) were marked differently than those caught at night (2100 and 0500). Solar midnight was at about 0145.

Chinook received a left partial pelvic fin clip if caught during the day and a right clip if caught at “night”. These marks were additional to a partial lower caudal clip that designated the middle site. A very small portion across the distal edge of the pelvic fins was cut. Pelvic fin clips were noticeable only if both fins were simultaneously lifted with a spatula and their lengths visually compared. Trap checkers at the downstream site depended on lower caudal fin clips (which were easily visible) to alert them to carefully check pelvic fins.

The fish were released immediately after work-up and recovery. Therefore, early in the season, “night” fish were released at about 0200 and 0600 and day fish at about 1400 and 1800. During most of the season after May 19th, fish were released at about 0600 and 1800. Theoretically, changing times of release would not effect heterogeneity due to a subpopulation effect, although it would help obscure any timing effect.

The lower site screw trap, as in previous years, was fished during the nighttime only. However, subpopulations with different tendencies to migrate during either the day or the night would still cause detectable heterogeneity in p at the lower site. For example, fish that tended to migrate during the day would be less available for nighttime capture at the lower site and would theoretically have a lower p than fish that migrated at night only (given adequate mixing).

As in the CJS experiment, losses on capture were not released and releases after June 9 at 0500 were discounted in the data. The cutoff times for the heterogeneity experiment were the same as for the CJS experiment.

When nighttime catch rates were high, and because the middle site was usually tended by one person, chinook smolts at the middle site were often measured during the daytime only. Nighttime measurements of chinook at the other two sites provided additional comparison. All fish were judged “smoltified” (silvery) or not. Scale-loss and injury data were unnecessary at the middle site, and chums were ignored to reduce time spent working up fish. Water temperature and turbidity were measured daily, and the U.S. Army Corps of Engineers measured discharge at the dam.

Recapture rates at the lower site for the two groups of fish were compared using a z test for difference in population proportions. Different recapture rates would indicate heterogeneity ($p_{d3} \neq p_{n3}$), given the assumption that the groups of day and night chinook had equal probabilities of survival ($\phi_{d2} = \phi_{n2}$). Lower site recapture rates were not pure estimates of capture probability, but were the products of survival probability between the middle and lower sites ($\phi_{.2}$) and capture probability at the lower site ($p_{.3}$). The z test was actually for

$$\phi_{d2}p_{d3} \neq \phi_{n2}p_{n3} .$$

Only if $\phi_{d2} = \phi_{n2}$ and cancel each other would the test purely detect heterogeneity in capture probability. An estimate of actual heterogeneity ($\hat{D}_3 = \hat{p}_{d3} - \hat{p}_{n3}$) would require estimates of $\phi_{.2}$ or $p_{.3}$. Only if survival rates were equal and perfect ($\phi_{d2} = \phi_{n2} = 1$) would the difference in lower site recapture rates equal the estimate of heterogeneity.

Video Observations

Fish behavior at the mouth of the inclined plane trap was observed with an underwater video monitor. When the inclined plane trap caught no chinook during the day, the main purpose was to determine if there was no daytime migration or if increased trap evasion was the cause. The monitor was placed at the bottom of the inclined plane, just inside and above the lip of the trap (Figure 9). A "sighting board" with depth marks spaced every 2 inches (5.08 cm), placed on the opposite side of the inclined plane, was used to measure the angle of elevation of fish passage. Horizontal distance from the monitor was estimated by comparing the distance of the fish to the corrugations of the metal plate lining the bottom of the inclined plane (Figure 9). Four troughs in the corrugated metal were visible from the monitor, with each trough spaced 1 foot (30.48 cm) further distant from the monitor. The estimate of horizontal distance (admittedly rough, especially for fish swimming high in the water column), combined with the angle of elevation from the sighting board, allowed for triangulation of elevation above the stream bottom of fish entering or leaving the trap. (Although judging horizontal distance was sometimes difficult, causing the triangulation method shown in Figure 9 to be less than ideal, I feel it was better than purely guessing the true elevation for each fish). Numbers of age-1 chinook that entered or escaped from the trap were tallied. Chum salmon smolts or age-0 chinook (indistinguishable from each other) were also counted. Other species were noted.

Simulations

PROC SIMULATE of Program RELEASE (Burnham et al. 1987) was used for computer simulations. The procedure generates expected capture history data (1's and 0's) from parameter values specified in the input. Parameters are for initial population size, and

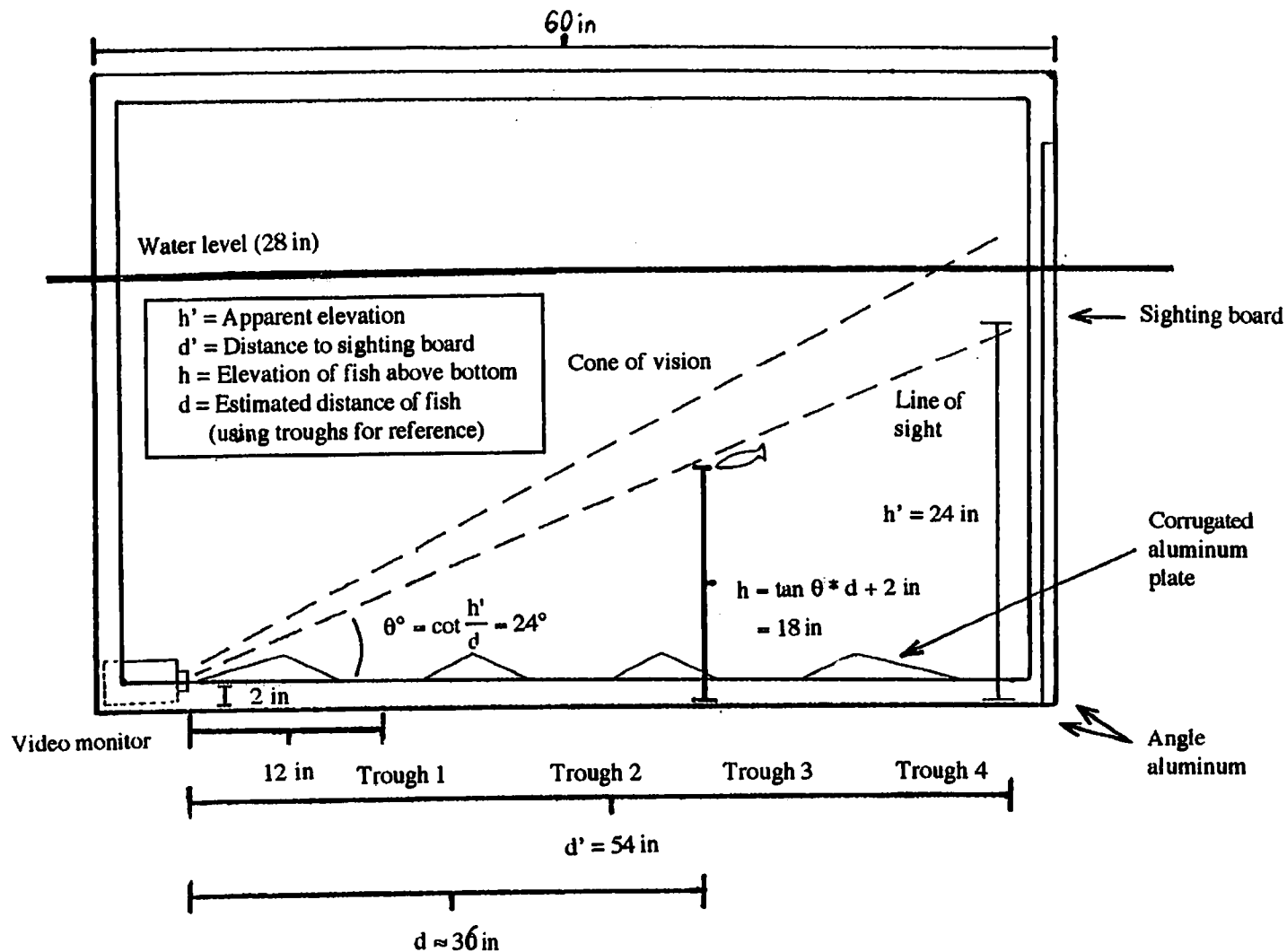


Figure 9. Video monitor placement (looking downstream into the trap mouth). The corrugated aluminum plate was flattened where joined to the angle aluminum, allowing clear visibility along the entire lip of the trap.

capture and survival probabilities, with different parameters assignable for subpopulations (see Appendix 3 for details of program input). The capture history data generated was pooled for the two groups and entered in Program JOLLY to get an abundance estimate.

Four scenarios were simulated, two with timing effects (at the lower site only, and at both the lower and middle sites) and two with subpopulation effects (heterogeneity at all three sites). One of the subpopulation scenarios had equal size subpopulations, and one had the day group (high p) one-third as large as the night group. There were eight simulations in each series, with heterogeneity increasing incrementally from zero. Percent relative bias and coverage were noted for estimates under Models A and A'. Because the simulated parameters and heterogeneity were based on results of the 1997 CJS and heterogeneity experiments, construction of the parameters are described in the results section.

Results

CJS Abundance Estimates

Capture histories for 1997 chinook salmon are in Table 2. Estimates under Model A, the general CJS Model with both death (emigration) and birth (immigration), and under Model A' (the Deaths Only Model) are in Table 3. The estimator for \hat{N}_i under Model A is defined for $i=2, \dots, k-1$, or for the middle site only (Pollock et al 1990). Under Model A', \hat{N}_i is defined for $i=1, \dots, k-1$, allowing an additional upper site estimate.

The only between-model test in the output of Program JOLLY that had sufficient data was between Model A and Model A' (although Models B and D were also specified in the input, see Pollock et al. 1990). The test statistic was $z = 2.023$ with probability = 0.0215, rejecting the null hypothesis that Model A' best fit the data.

The fact that there are no tributaries large enough to support salmon entering the study reach and almost all chinook spawn upstream (Peterson 1997) did not necessarily disqualify Model A (both death and birth). Outmigrants positioned between the upper and lower sites at the start of sampling, both those primarily feeding and rearing and those actively migrating, would in effect be additions to the population (recruits). The study reach appears to be good rearing habitat for chinook juveniles, with large woody debris,

Table 2. Capture histories of chinook salmon, 1997. A "1" represents marked fish captured and a "0" represents marked fish not captured (e.g., 110 represents marked fish captured at the upper and middle sites, but not at the lower site). Unhealthy or dead fish were not released and were entered as losses on capture in program JOLLY. Chinook caught at the middle site between 0900 and 1700 on June 10 probably did not have enough time to reach the lower site trap before high water and debris forced stopping the trap there at 0130 on June 10. These fish were also entered as "losses on capture".

	<u>Capture History:</u>			<u>Numbers of Chinook:</u>	
		Releases	Losses on Capture	Insufficient Travel Time to Lower Site	
100		2205	41	-	
010		2321	41	39	
001		3303	-	-	
110		46	3	2	
101		48	-	-	
011		39	-	-	
111		0	-	-	

Table 3. Population estimates, SE's and coefficients of variation for chinook salmon, 1997, under Models A and A'.

Parameter	Estimate	SE	CV	Lower Bound	Upper Bound
<u>Model A (Deaths and Immigration)</u>					
N(2)	135,051	33,735	0.25	68,930	201,172
<u>Model A' (Deaths Only)</u>					
N(1)	133,468	12,936	0.10	108,113	158,823
N(2)	199,302	31,047	0.16	138,450	260,154
Average N	166,385	16,817	0.10	133,424	199,346

cut banks and deep holes. Higher numbers of actively migrating chinook would probably be positioned within the study reach if the experiment were to begin at a time when fish from upriver reaches were migrating through at a high rate. This was probably the case [Figure 7]).

Normally, because the between-model test rejected Model A' for the more complex Model A and "recruitment" may have existed, Model A would automatically be the best model choice. In this case, however, the bias resulting from incorrect model choice must be weighed against bias due that could result from heterogeneity in capture probability.

The only goodness-of-fit (GOF) test with sufficient capture histories or occasions was Component 2 under Model A'. The test (shown in Table 4) failed to reject the null hypothesis that Model A' fit the data sufficiently well ($\chi^2 = 3.637$, 1 df, probability = 0.0565), although barely so. Although test power was probably low (there were only three capture occasions with low capture probabilities), this indicates that Model A' fit the data sufficiently well.

An estimate of "recruitment" for 1997 was not possible under Model A. The estimator for \hat{B}_i is defined on occasions $i=2, \dots, k-2$, requiring at least four occasions or trapping sites.

One peculiarity was that the Deaths Only Model estimated $\hat{N}_1 = 133,468$ and $\hat{N}_2 = 199,302$ without recruitment, a higher population at the middle site compared to the upper site would, of course, be impossible. Possible reasons are considered in the discussion.

Table 4. Component 2 contingency table goodness-of-fit test under Model A' for chinook salmon, 1997 . The test barely failed to reject the null hypothesis that Model A' sufficiently fit the data. Because there were only $i=3$ occasions and the two left columns could not be filled, test power was probably low.

I = 2:	First captured before i-1, not captured in i-1		First captured in i-1	First captured after i-1
	Captured in i	0	0	52.00
Expected value	Expected value	0	0	42.65
	Captured after, not in i	0	0	48.00
Expected value	Expected value	0	0	57.35

Chi = 3.6369, df = 1, p = 0.0565

Heterogeneity experiment

The lower site recapture rates for “day” and “night” chinook were:

$$\rho_{d3} = 21 / 636 = 0.0330 \text{ and}$$

$$\rho_{n3} = 17 / 1724 = 0.0098 .$$

A two-tailed z test for difference between two population proportions was significant at the 99% confidence level ($Z=3.97$, $z_{0.01/2}=2.58$, $p<0.0001$). If the assumption of $\phi_{d2} = \phi_{n2}$ were met, the z test indicated heterogeneity in capture probability at the lower site. The estimated difference between recapture rates would be an estimate of heterogeneity only if $p_d = p_n = 1$. If ϕ_{d2} and ϕ_{n2} were equal and perfect, the estimate of heterogeneity would be:

$$\begin{aligned} \hat{D}_3 &= \rho_d - \rho_n \\ &= 0.0330 - 0.0098 \\ &= 0.0231 \end{aligned}$$

with a standard error of

$$\begin{aligned} SE &= \sqrt{\frac{\hat{p}_d(1 - \hat{p}_d)}{n_d} + \frac{\hat{p}_n(1 - \hat{p}_n)}{n_n}} \\ &= \sqrt{5.0200 \times 10^{-5} + 5.663 \times 10^{-6}} \\ &= 0.007474 . \end{aligned}$$

The 95% confidence interval ($z_{0.05/2} = 1.96$) would be

$$0.0085 \leq D_3 \leq 0.0379 .$$

Maximum likelihood estimates of p_{d3} and p_{n3} and heterogeneity ($\hat{D}_3 = \hat{p}_{d3} - \hat{p}_{n3}$) were not possible, because $\hat{\phi}_i$ is defined for $i=1, \dots, k-2$ and \hat{p}_i for $i=2, \dots, k-1$ under Model A and the parameters in the recapture rates are confounded ($\rho_{.3} = \hat{\phi}_2 \hat{p}_3$). The single,

all-occasion survival estimate from CJS Model B, a simplification of Model A with constant survival probability (Pollock et al. 1990), would allow estimation of p_{d3} and p_{n3} . There was, however, no justification for choosing Model B in the output from JOLLY, and the Model B survival estimate was too poor and imprecise to be useful ($\hat{\phi} = 1.28$, SE = 0.27, CI: 0.75 to 1.80).

Heterogeneity also appeared to exist at the middle site. Fish caught and marked at the upper site (during the night) were, relative to unmarked fish, more likely to be captured during day at the middle site than at night. Fish with upper site marks made up 3.3% of the seasonal daytime catch at the middle site (22 out of 666), and only 1.6% of the nighttime catch (29 out of 1757, accounting for middle site losses on capture). The null hypothesis of equal proportions of upper site-marked and unmarked fish captured at the middle site during the day compared to the same proportion at night was strongly rejected with a chi-square contingency table test:

	Middle Site Day Captures	Middle Site Night Captures
Marked at Upper Site	22	29
Unmarked	644	1757

chi-square = 6.7190, df = 1, and p = 0.0095 .

The result suggests heterogeneity in p at the middle site between upper site-marked and unmarked fish. Upper site-marked fish were overrepresented in the middle site day catch and (from the z-test results) the middle site day catch was over-represented in the lower site catch. This could have resulted from a common subpopulation being over-represented (having higher p_i) at both sites. The alternative would be back-to-back timing

effects at the middle and lower sites, with relatively high p 's for upper site-marked fish at the middle site during the day and middle site "day" fish at the lower site at night.

Under a subpopulation scenario, one would expect similar daytime proportions of upper site-marked to unmarked fish at the middle and lower sites (given high ϕ 's and a relatively undiminished population between sites). Because the lower site trap was not fished (or effective) during the day, this test was not possible. However, the relative proportions of marked to unmarked fish caught during the night can be compared between the middle and lower sites:

	Middle Site Night Captures	Lower Site Night Captures
Marked at Upper Site	29	48
Unmarked	1757	3341

$$\text{chi squared} = 0.3432, \text{ df} = 1, p = 0.5580 .$$

The test did not reject the null hypothesis that the proportions of marked to unmarked fish did not change between the middle and lower sites at night, even though mortality could have affected the lower site proportion. This suggests that upper site-marked fish were well-mixed with unmarked fish, at least by the time they arrived at the middle site at night. If they were not well mixed, the proportion would probably have changed between sites as marked fish became more evenly distributed in the river. The power of the test, however, or the probability of rejecting the null hypothesis given it were false (having a chi-square statistic ≥ 3.84) was quite low (power = 0.50, from Table 3.4 in Burnham et al. [1987]).

Although the above test between middle and lower site night catches detected no difference, a similar test between the middle site day and the lower site at night was significant:

	Middle Site Day Captures	Lower Site Captures (Night)
Marked at Upper Site	22	48
Unmarked	644	3341

chi squared = 11.6825, df = 1, $p = 0.0006$.

Thus, marked and unmarked fish seemed to be well-mixed in the nighttime comparison, but not in the day-night comparison, even though fish had to have traveled the same stretch of river. The combined tests seem to suggest a subpopulation effect, but the possibility of back-to-back timing effects is not disproved. For example, fish marked at the upper site at night could have had a tendency to arrive at the middle site during the day (say within 12 hours) and, similarly, fish caught and marked during the day at the middle site could have had a tendency to arrive at the lower site less than 12 hours later at night. Upper site-marked fish would then be over-represented at the middle site during the day, and fish marked during the day at the middle site would be over-represented at the lower site.

Knowing the average travel time for chinook between sites could suggest one or the other scenario, with a short time favoring a timing effect and longer time favoring a subpopulation effect. Although fish were not individually marked, some travel time information is available. In 1997, chinook were first marked on May 6 at the upper site. The lower site, 15.8 km downstream, first captured upper site-marked chinook (3 of them) three days later on May 9, and had fished full nights since May 7. The middle site was not fishing until May 9 as well, and immediately began capturing marked fish. In a small

experiment on May 21 and 22, 98 and 97 upper site chinook (respectively) were given right partial pelvic fin clips in addition to upper caudal clips. Two of these were recaptured at the lower site on May 23, for a travel time of 1 to 2 days through the study reach. Strangely, 2 were captured at the middle site on May 24, one during the day and 1 at night, for 2 - 3 days travel between the upper and middle sites. In 1996, chinook were first marked at the upper site on May 7, first recaptured at the lower site (1 fish) on May 8, and first recaptured at the middle site (1 fish) on May 9 (Peterson 1997). The lower site in both years had higher capture rates than the middle site, possibly accounting for first capture at the lower site in two of the above instances. All considered, the first chinook took from 12 hours to 3 days to travel between sites. Without knowledge of the rate of mixing over time and distance, the sparse travel time information cannot really point to either a timing or subpopulation effect.

Released chinook kept in tight schools, at least until swimming out of view (about 20 m during daytime at the middle site). They usually seemed to be well dispersed (mixed with unmarked fish) before reaching the next downstream site, but not always. For the first 20 days of the season (before upper site capture rates plummeted to almost nothing on May 27, Figure 10), the average number of upper site releases per 3 hour period was 36.8 (SD = 20.1). Middle site recaptures per 8 hour period (or pooled 4 hour periods) were generally quite low and evenly distributed, with two glaring exceptions:

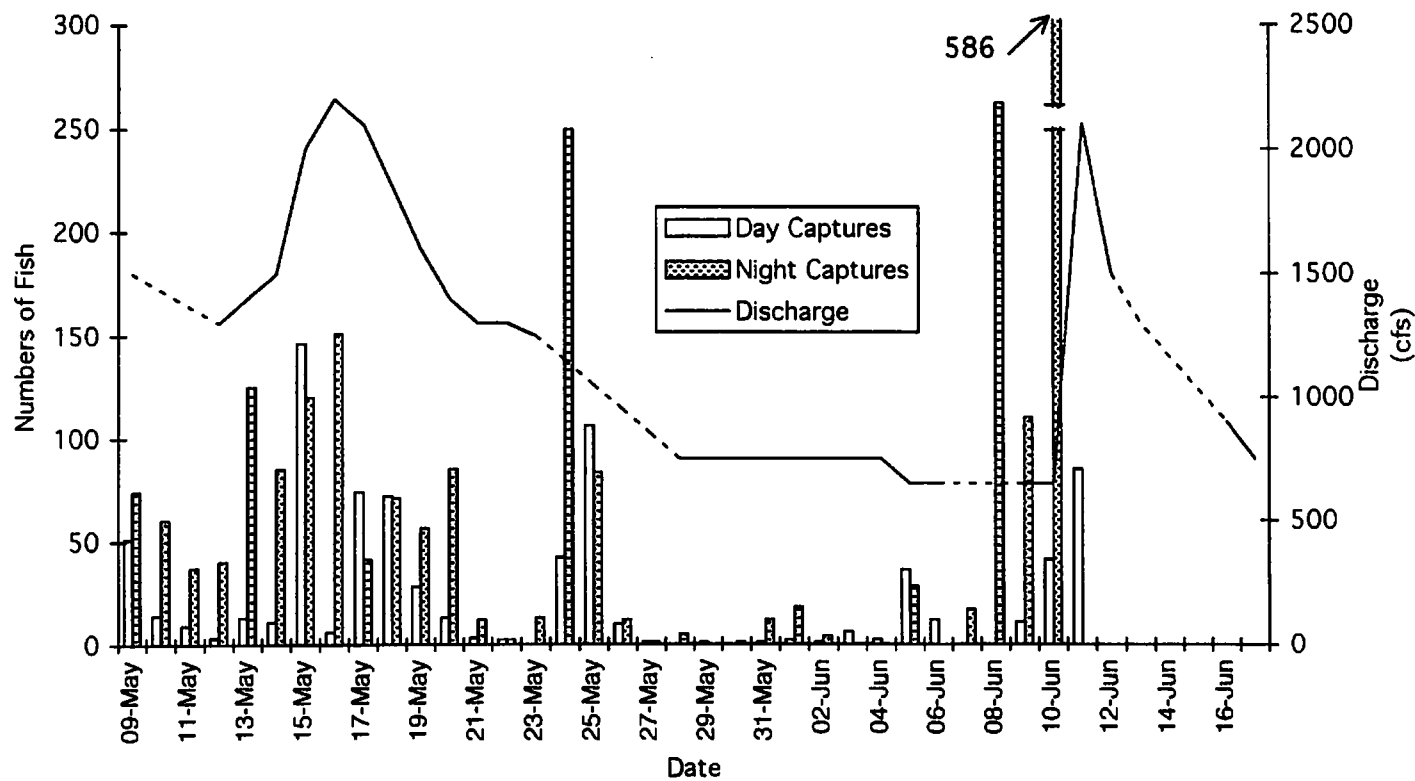


Figure 10. Day and night chinook captures at the middle site, 1997, and discharge. Discharge was measured by the U.S. Army Corps of Engineers at the dam. Dashed lines represent no data taken.

Middle Site Recaptures per Period (day or night)	Number of Instances (entire season)
0	60
1	13
2	6
3	2
10	2

The two periods with 10 recaptures were back-to-back, on May 24 at night and May 25 during the day (both were 8 hour periods, see Appendix 2), and were part of a large, anomalous spike in middle site capture rates for unmarked fish as well (Figure 10). Marked fish comprised $23 / 1394 = 0.0165$ of the total middle site catch during May 9 - 23. The ratios on the May 24 and 25, especially on the latter, were relatively high ($10 / 239 = 0.0418$ and $10 / 96 = 0.0104$, respectively). Speculatively, the high percentages could have been caused by released marked fish sometimes, but not always, remaining in schools after release. Marking could also have caused fish to slow or temporarily cease migration and stack up between the upper and middle sites.

The May 24-25 spike was not obviously related to discharge (Figure 10) or water temperature (Figure 11). Perhaps coincidentally, the spike was on Memorial Day Weekend when boat traffic was very heavy, causing the water to become visibly turbid during the day (Figure 12). Turbidity was < 7 units ($\times 100$ ppm silica equivalents) in the morning (below the detection limit) and 11 to 12 units in the afternoon. The weather was partly cloudy and warm during the day and clear with frost at night.

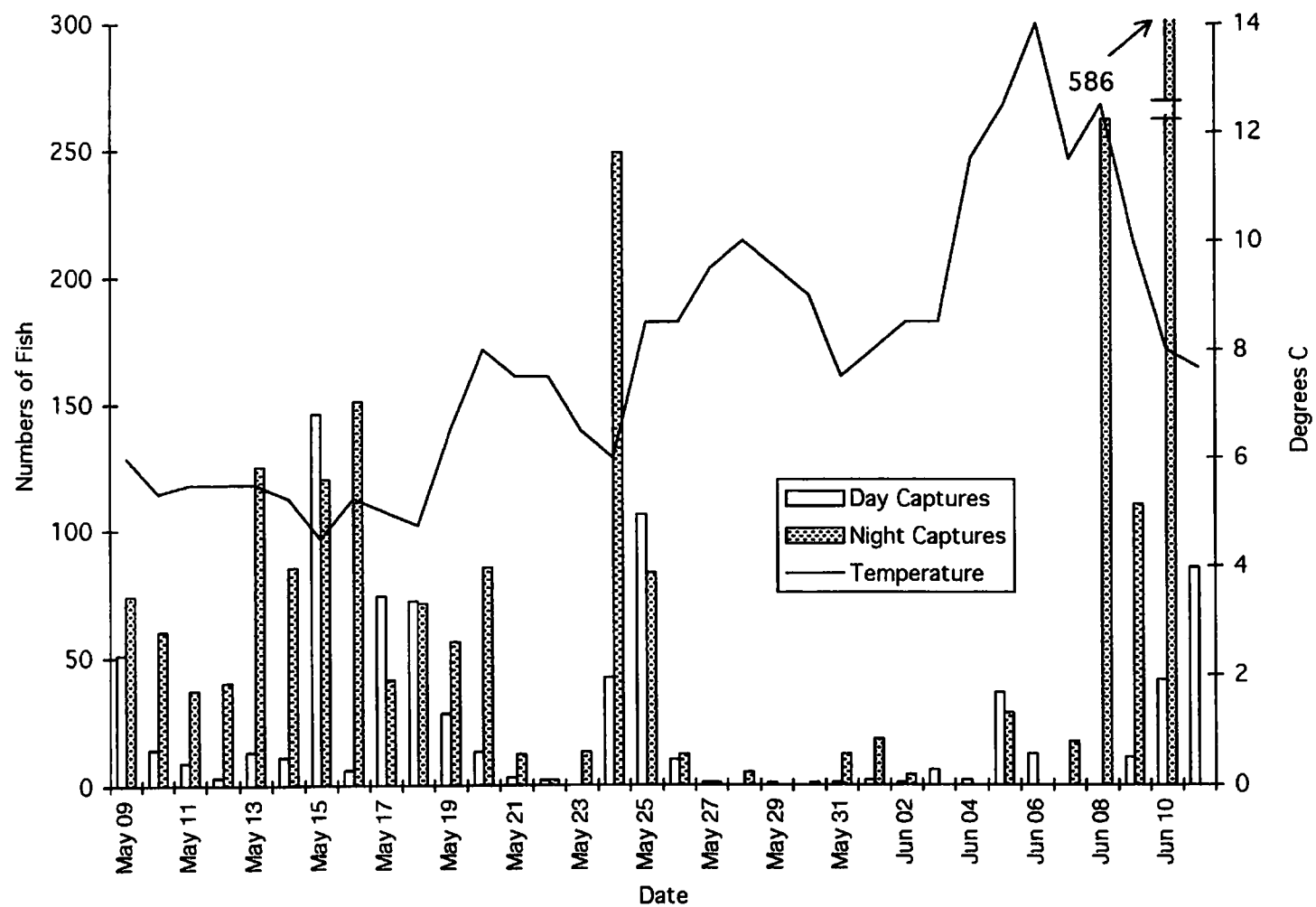


Figure 11. Chinook captures (day and night) and temperature at the middle site, 1997.

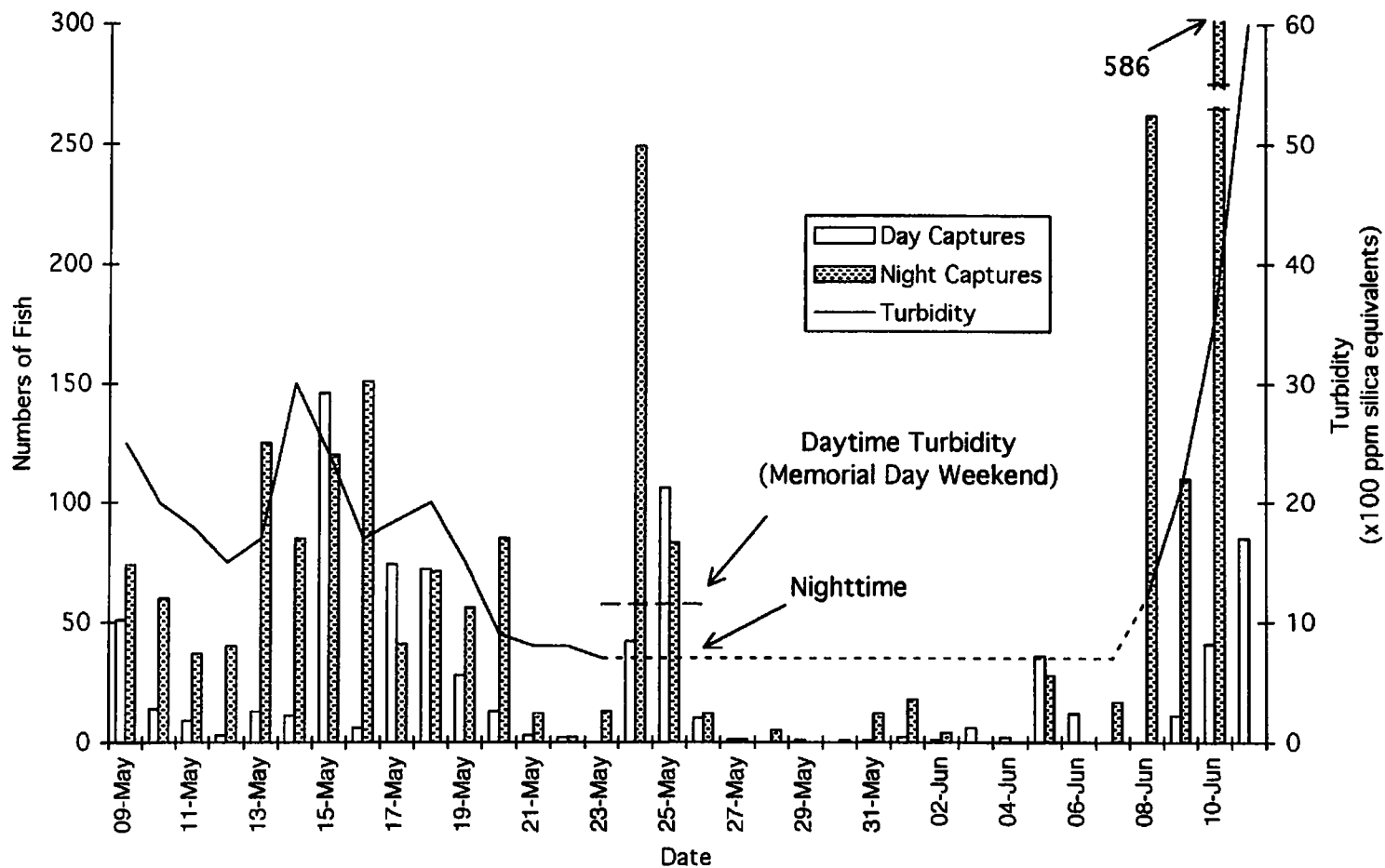


Figure 12. Chinook captures, day and night, and turbidity at the middle site, 1997. Turbidity was measured with the U.S. Geological Survey platinum-wire method. The dashed line represents the minimum detection level of ≤ 7 units.

Turbidity in general seemed to trigger outmigration before increased discharge. After heavy rains on the night of June 7, both turbidity and catch rates increased before discharge. (I observed a similar, but less marked example of this in 1998. Rains caused small, but very turbid intermittent streams to color the lower river before relatively large volumes of water arrived from the upper drainage.) On the night of June 8 (ending on 0500 on June 9) at the middle site, 262 chinook were captured compared to 17 on the previous night. Turbidity had increased during the night from < 7 to 12 units. Discharge had not increased from the pre-storm level of 650 cfs. Water level, observed at the middle site, did not begin increasing until afternoon on June 10 (after which it rose very quickly). The U.S. Army Corps of Engineers measurements were 650 cfs at 0815 on June 10, and increased to 2100 cfs by 0820 on June 11.

A difference in general physical appearance or average length between chinook caught during the day and at night could potentially indicate different subpopulations. All chinook at the middle site were judged as smolted (silvery, with indistinct parr marks) or not. However, most smolts displayed a gradation of silver color and parr marks, with no obvious cut-off point. The judging was very subjective, varied among personnel, and was probably affected by nighttime lantern light. However, there were no obvious differences between the appearance of night and day chinook.

Because only one person was working-up fish or setting the trap at the middle site (having to do one or the other every 4 hours in the early season), and because nighttime catches were often high, forklength was not measured at night at the middle site for much of the season. None of the four available middle site day/night comparisons (on May 9, May 28 - June 4 [pooled], June 5 and June 10) were significant (Table 5).

Table 5. Middle site comparisons of average fork length between chinook captured during the day and at night. None of the two-tailed t tests ($\alpha = 0.05/2$) were significant.

Date	<u>Number Measured</u>		<u>Average Length (SD)</u>		P
	Day	Night	Day	Night	
May 9	50	100	74.66 (5.41)	75.61 (6.99)	0.3609
May 28-June 4	11	44	79.55 (5.28)	79.57 (5.24)	0.9900
June 5	35	28	81.43 (5.49)	79.25 (5.57)	0.1259
June 10	30	30	83.53 (6.47)	80.76 (6.15)	0.0948

Video Observations

The results are in Table 6, and the raw data is in Appendix 2. In all 13 h, 7 min. of video was recorded, 8 h, 25 min. at night and 4 hr 42 min. during the day. Chinook smolt were clearly visible and easy to differentiate from age-0 chinook by their relatively large average size of (79 to 84 mm between May 28 and June 10). In contrast, chum fry averaged 39 mm (in 1996, Daigneault 1997) and age-0 chinook were approximately the same size.

No chinook entered the trap during the day, probably because overall capture rates were very low between May 31 and June 10 (Figure 12). A total of 122 chinook smolt were counted entering the trap mouth, and 87 leaving (from approximately 1 to 20 s later). Chinook entered the trap at an average elevation of 25 cm above the river bottom, and escaped at 8 cm above bottom where the water was slower (the lip of the trap was 5 cm above river bottom, so they escaped about 3 cm above the trap lip). The 71% observed escaping is probably misleading since the cone of vision only covered about half of the trap entrance (Figure 9), but covered almost the entire lower part of the trap, where most of the fish escaped. A conservative estimate of escapement would therefore be around 35 percent. Chinook were seen swerving away from the trap to avoid entrance, or holding on the

Table 6. Inclined plane trap video data, middle site, 1997. Age-0 chum and chinook salmon were indistinguishable from each other.

Date	Day or night	Time		Number		Average Elevation		Total
		Start	Stop	Age-1 Chinook: Entering Leaving		of Chinook (cm): Entering Leaving		
May 31	Day	1530	1707	0	0	-	-	24
May 31	Night	2130	2219	0	0	-	-	11
June 2	Day	1200	1303	0	0	-	-	0
June 3	Night	0215	0405	0	0	-	-	0
June 5	Night	0145	0248	2	3	33	5	3
June 5	Day	1230	1332	0	0	-	-	3
June 5	Night	2100	2232	0	0	-	-	5
June 7	Night	2220	2324	11	7	23	10	3
June 8	Day	0900	1000	0	0	-	-	5
June 9	Night	0025	0132	108	76	25	8	25
June 9	Night	2100	2200	1	1	18	8	15
June 10	Night	0300	0400	Too much turbidity for viewing.				
Total				122	87	25	8	94

bottom in the cushion of slow water in front of the trap lip. No age-0 chum or chinook salmon escaped; these fish were observed at about equal frequencies during the day and night. Almost all fish entered tail-first, the age-1 chinook at much slower speeds (they were better able to fight the current). Chinook traveled mostly in schools of 3 to 20 fish, while age-0 salmon were almost always seen alone or in groups of 2 or 3. Water velocity was not measured at the trap, but was probably between 1.0 and 1.5 m/s.

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Simulations

The four scenarios were:

Scenario A: heterogeneity at the lower site only, due to a timing effect between day and night, middle site-marked fish;

Scenario B: heterogeneity at the middle and lower sites, due to timing effects;

Scenario C: heterogeneity between subpopulations of “day” and “night” groups of chinook (at all sites), with equal-sized subpopulations; and

Scenario D: heterogeneity between subpopulations, with the day group numbering only 1/3rd of the night group.

Eight simulations were carried out for each scenario. A “0” or base simulation with no heterogeneity, a simulation with all induced heterogeneity close to the apparent, observed level at the 1997 lower site (simulation “1”), and simulations with heterogeneity increased by increments of 0.02 (simulations 2-7). Assigned parameters are in Table 7.

Table 7. Parameter specifications for simulations A1 through D1. All "1" simulations had heterogeneity at the lower site equal to the observed level at the lower site ($i = 3$) in 1997 for chinook salmon. Simulations B1 - D1 used the 1997 observed lower site heterogeneity at the middle and upper sites as well. Base simulations ("0" series, not shown) substituted the weighted average of observed lower site recapture rates adjusted for assumed $\phi(.2)=0.95$, or $p(.3)=0.02257$. Runs 1 - 7 increased $p(\text{day})$ by increments of 0.02.

Parameter	"Day" Chinook	"Night" Chinook
<u>A Simulations: timing effect at lower site only</u>		
$\phi(1)$	0.95	0.95
$\phi(2)$	0.95	0.95
$p(1)$	0.0142	0.0142
$p(2)$	0.0226	0.0226
$p(3)$	0.0348	0.0104
$N(1)$	82,500	82,500
<u>B Simulations: equal timing effects at middle and lower sites</u>		
$\phi(1)$	0.95	0.95
$\phi(2)$	0.95	0.95
$p(1)$	0.0142	0.0142
$p(2)$	0.0348	0.0104
$p(3)$	0.0348	0.0104
$N(1)$	82,500	82,500
<u>C Simulations: equal subpopulations of "day" and "night" fish</u>		
$\phi(1)$	0.95	0.95
$\phi(2)$	0.95	0.95
$p(1)$	0.0348	0.0104
$p(2)$	0.0348	0.0104
$p(3)$	0.0348	0.0104
$N(1)$	82,500	82,500
<u>D Simulations: subpopulation "day" fish = 1/3rd "night"</u>		
$\phi(1)$	0.95	0.95
$\phi(2)$	0.95	0.95
$p(1)$	0.0348	0.0104
$p(2)$	0.0348	0.0104
$p(3)$	0.0348	0.0104
$N(1)$	41,250	123,750

All scenarios had an initial population size of $N_1 = 165,000$. This number is close to the average of \hat{N}_1 and \hat{N}_2 under Model A' in 1997 ($\hat{N}_{ave} = 166,000$ SE = 17,000) and in 1996 ($\hat{N}_{ave} = 172,000$, SE = 13,000). Day and night chinook were given equal subpopulation sizes for Scenarios A through C, and the day group was 1/3rd the size of the night group for Scenario D. All ϕ 's were set at 0.95.

Capture data from the 1997 experiment was used where possible in an effort to approximate real (but unknown) capture probabilities. Assigned upper site capture probability was

$$\begin{aligned} p_1 &= \frac{\text{upper site captures}}{N_1} \\ &= \frac{2345}{165,000} \\ &= 0.0142. \end{aligned}$$

For p_2 , the assumed, constant $\phi_1 = 0.95$ was factored in:

$$\begin{aligned} p_2 &= \frac{\text{middle site recaptures}}{\text{upper site releases}} \div 0.95 \\ &= \frac{51}{2304} \div 0.95 \\ &= 0.0233. \end{aligned}$$

For all occasions where heterogeneity was induced,

$$\begin{aligned} p_3 &= \frac{\text{Lower site recaptures of day fish}}{\text{middle site releases of day fish}} \div 0.95 \\ &= \frac{21}{636} \div 0.95 \end{aligned}$$

$$=0.0348$$

and, likewise for night fish,

$$p_{n3} = \frac{17}{1724} + 0.95$$

$$= 0.01038.$$

The above parameters were for the base (“1”) simulations. Six more simulations were carried out, increasing p_{d3} incrementally by 0.02 for each.

Population estimates from the general CJS model (Model A, with death and immigration) and the deaths-only model (Model A’) (Pollock et al 1990) were recorded from Program JOLLY (Table 8). Percent bias was calculated for each simulation, classified as low ($< 2.5\%$), medium ($2.5\% \leq$ and $< 10\%$) or high ($\geq 10\%$), and coverage was noted (Table 9).

Abundance estimators under Model A and Model A’ were very robust to heterogeneity in the final capture occasion (Scenario A, Figure 13). Simulation A7, with the greatest heterogeneity ($p_{d3} = 0.1548$ and $p_{n3} = 0.0104$), had bias in the “low” range and N was covered for all estimates (Table 9). Precision of the estimates actually improved from A0 to A7 and bias did not substantially increase, because p_{d3} (and the number of recaptures) increased with increasing heterogeneity.

In Scenario B, with heterogeneity at the lower and middle sites (back-to-back, equal timing effects), the Model A’ estimator for N_1 remained robust (Figure 14). In contrast, negative bias asymptotically increased with increasing heterogeneity in the estimates of N_2 under Model A and Model A’. In Simulation B1, with bias at a similar level to the observed

Table 8. Abundance estimates and SE's for simulations under Scenarios A through D. "True" $N(1) = 165,000$ and $N(2) = 156,750$.

Simulation	Model A', $N(1)$	SE	Model A', $N(2)$	SE	Model A, $N(2)$	SE
<u>A Simulations</u>						
0	160,578	15,291	154,740	17,356	151,682	33,579
1	165,051	15,962	154,651	17,346	154,110	34,501
2	165,051	15,962	154,651	17,346	154,110	34,501
3	165,528	13,284	155,920	12,627	154,708	28,922
4	165,265	12,294	156,603	11,376	155,847	27,738
5	165,012	11,480	156,356	10,345	155,961	26,756
6	164,823	10,796	156,818	9,598	156,668	26,137
7	165,313	10,276	156,100	8,885	155,344	25,341
<u>B Simulations</u>						
0	160,484	15,282	154,565	17,336	151,343	33,503
1	166,094	16,147	120,112	11,787	117,981	25,571
2	164,224	13,131	106,719	6,697	105,699	17,898
3	165,169	11,524	99,528	4,522	98,807	14,140
4	165,084	10,312	95,147	3,354	93,802	11,736
5	164,565	9,360	92,322	2,639	91,170	10,189
6	164,706	8,665	90,329	2,158	89,714	9,115
7	164,468	8,069	88,773	1,810	88,112	8,210
<u>C Simulations</u>						
0	163,835	12,778	154,386	17,316	151,924	29,222
1	127,269	8,671	120,148	11,790	119,000	19,990
2	112,897	4,900	106,762	6,698	105,947	11,332
3	105,213	3,292	99,544	4,519	98,774	7,618
4	100,761	2,436	95,288	3,356	94,575	5,639
5	97,639	1,903	92,332	2,632	91,504	4,398
6	95,537	1,547	90,338	2,150	89,589	3,580
7	93,924	1,290	88,808	1,801	88,029	2,986
<u>D Simulations</u>						
0	163,079	12,676	154,609	17,341	154,188	29,597
1	116,705	10,525	109,286	14,144	106,258	23,627
2	91,306	5,469	86,167	7,444	84,416	12,461
3	78,710	3,475	74,059	4,721	72,396	7,866
4	70,664	2,429	66,507	3,312	65,014	5,499
5	65,659	1,873	61,748	2,508	60,406	4,151
6	62,024	1,445	58,290	1,981	56,949	3,263
7	59,347	1,176	55,726	1,618	54,426	2,654

Table 9. Percent bias and coverage of simulated estimates under Scenarios A through D. Classifications of percent bias were low (<2.5), medium (≥ 2.5 and <10.0) and large (≥ 10.0). Coverage considered whether the estimate fell within the 95% confidence interval.

Simulation Number	<u>Model A', N(1)</u>			<u>Model A', N(2)</u>			<u>Model A, N(2)</u>		
	% Bias	Bias Class	Coverage? (Y or N)	% Bias	Bias Class	Coverage? (Y or N)	% Bias	Bias Class	Coverage? (Y or N)
<u>A Simulations</u>									
0	-2.680	M	Y	-1.282	L	Y	-3.233	M	Y
1	0.031	L	Y	-1.339	L	Y	-1.684	L	Y
2	0.031	L	Y	-1.339	L	Y	-1.684	L	Y
3	0.320	L	Y	-0.530	L	Y	-1.303	L	Y
4	0.161	L	Y	-0.094	L	Y	-0.576	L	Y
5	0.007	L	Y	-0.251	L	Y	-0.503	L	Y
6	-0.107	L	Y	0.043	L	Y	-0.052	L	Y
7	0.190	L	Y	-0.415	L	Y	-0.897	L	Y
<u>B Simulations</u>									
0	-2.737	M	Y	-1.394	L	Y	-3.449	M	Y
1	0.663	L	Y	-23.374	H	N	-24.733	H	Y
2	-0.470	L	Y	-31.918	H	N	-32.568	H	N
3	0.102	L	Y	-36.505	H	N	-36.965	H	N
4	0.051	L	Y	-39.300	H	N	-40.158	H	N
5	-0.264	L	Y	-41.102	H	N	-41.837	H	N
6	-0.178	L	Y	-42.374	H	N	-42.766	H	N
7	-0.322	H	N	-43.367	H	N	-43.788	H	N
<u>C Simulations</u>									
0	-0.706	L	Y	-1.508	L	Y	-3.079	M	Y
1	-22.867	H	N	-23.351	H	N	-24.083	H	Y
2	-31.578	H	N	-31.890	H	N	-32.410	H	N
3	-36.235	H	N	-36.495	H	N	-36.986	H	N
4	-38.933	H	N	-39.210	H	N	-39.665	H	N
5	-40.825	H	N	-41.096	H	N	-41.624	H	N
6	-42.099	H	N	-42.368	H	N	-42.846	H	N
7	-43.076	H	N	-43.344	H	N	-43.841	H	N
<u>D Simulations</u>									
0	-1.164	L	Y	-1.366	L	Y	-1.634	L	Y
1	-29.270	H	N	-30.280	H	N	-32.212	H	N
2	-44.663	H	N	-45.029	H	N	-46.146	H	N
3	-52.297	H	N	-52.753	H	N	-53.814	H	N
4	-57.173	H	N	-57.571	H	N	-58.524	H	N
5	-60.207	H	N	-60.607	H	N	-61.463	H	N
6	-62.410	H	N	-62.813	H	N	-63.669	H	N
7	-64.032	H	N	-64.449	H	N	-65.278	H	N

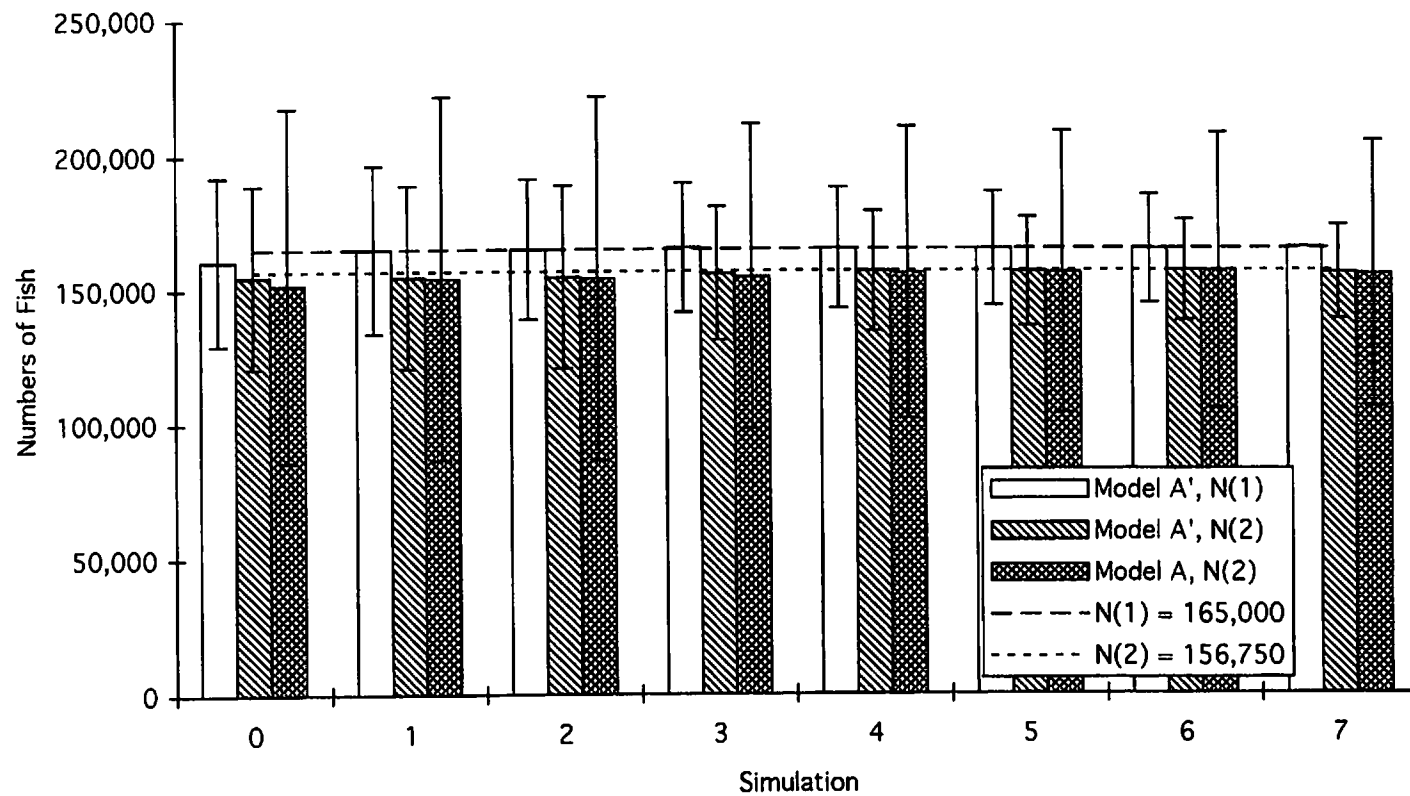


Figure 13. Simulation abundance estimates under Scenario A (heterogeneity due to a timing effect at the lower site only). True populations and 95% confidence intervals are shown.

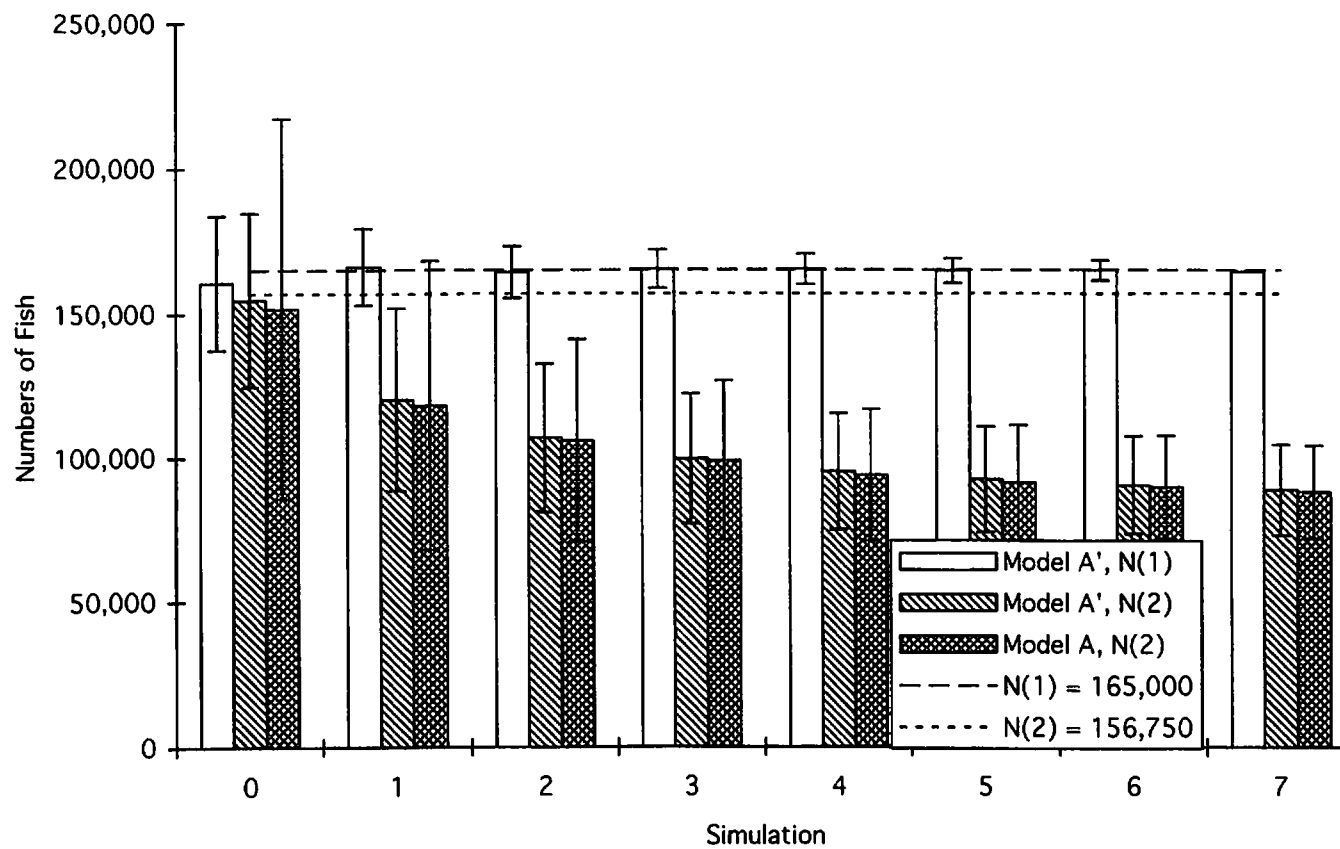


Figure 14. Simulation abundance estimates under Scenario B (timing effects at the middle and lower sites).

difference in recapture rates for day and night fish, the Model A' estimate of $N(1)$ had low bias and had coverage. The other estimates had high negative bias ($>23\%$) (Table 9), although \hat{N}_2 under Model A barely had coverage.

All estimates in scenarios C and D, with heterogeneity at all sites due to a subpopulation effect, had high bias and poor coverage. Percent bias ranged from 23% to 32% in the estimates with heterogeneity similar to what may have existed in the Chena CJS experiments. Bias was less severe in Scenario C, for which the day and night subpopulations had equal size, than in Scenario D for which the day group was 1/3rd of the night (Figures 15 and 16).

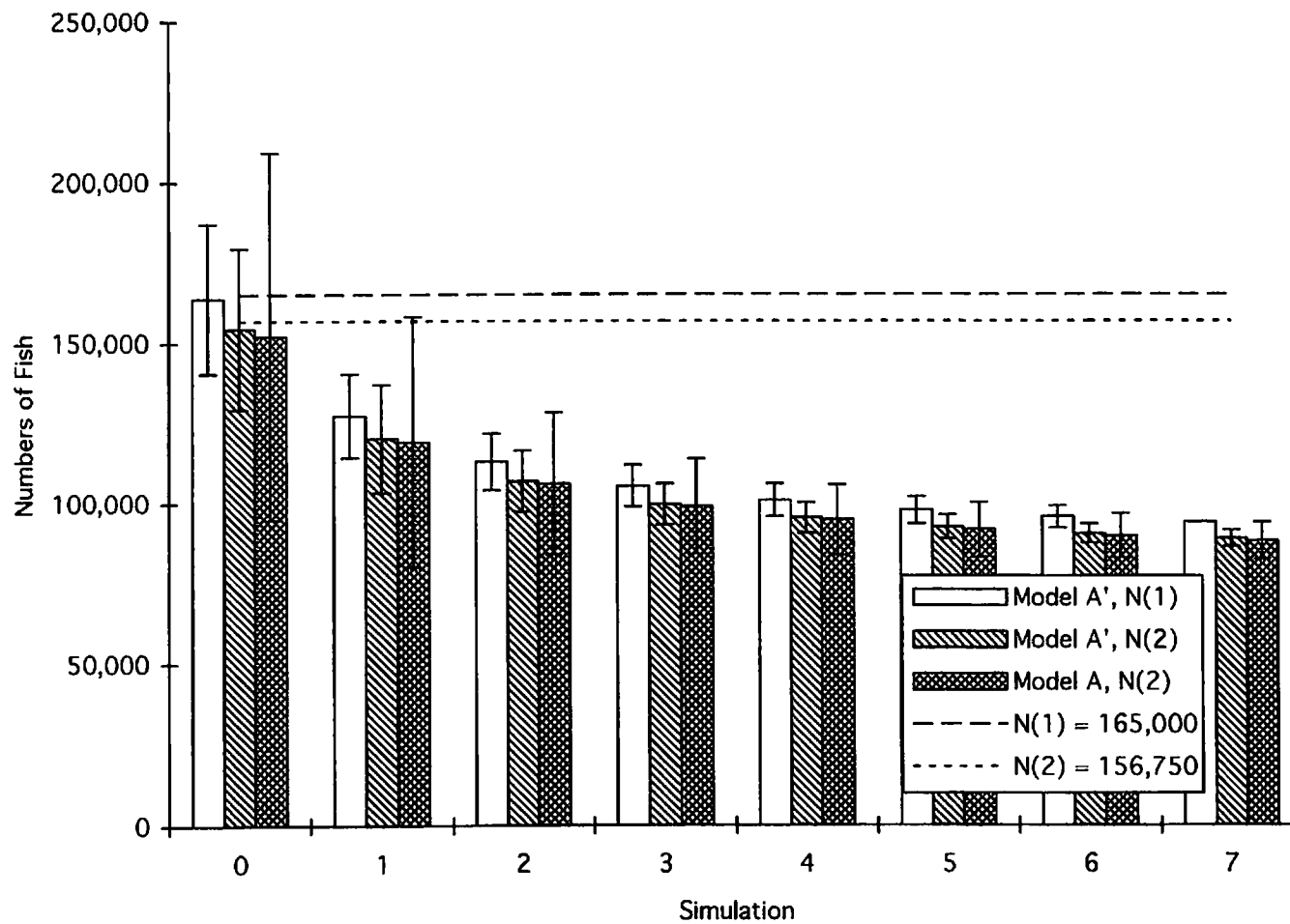


Figure 15. Simulation abundance estimates under Scenario C (heterogeneity at all sites, equal-size subpopulations).

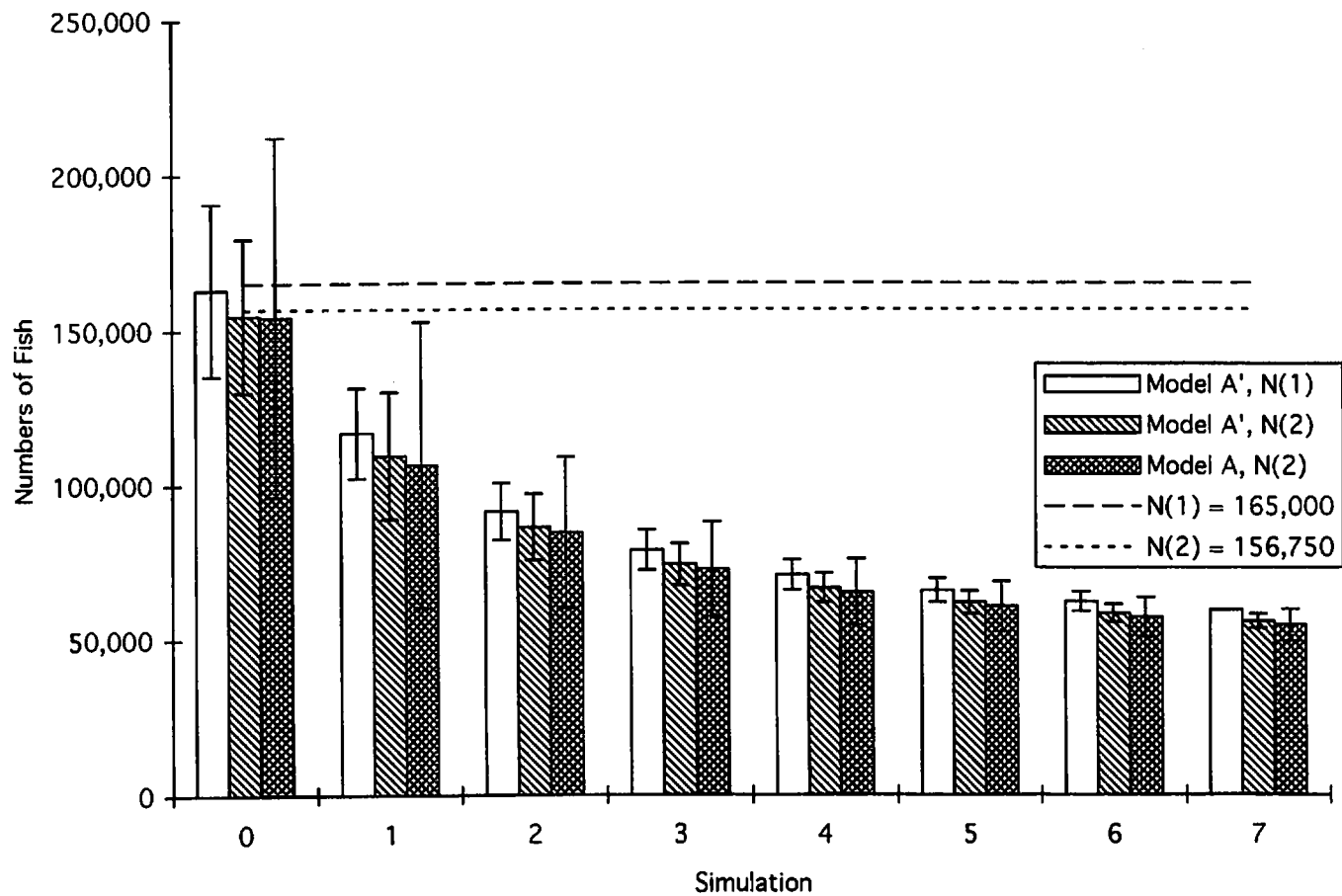


Figure 16. Scenario D estimates (heterogeneity at all sites, with the day group [higher p] 1/3rd the size of the night group).

Discussion

Existence and Level of Heterogeneity

The z test of the heterogeneity experiment showed that lower site recapture rates for the day and night groups of chinook were different (probability < 0.001). Whether the difference was due to heterogeneity in p is less certain and depends on the assumption of equal survival probabilities for the day and night groups.

Because day and night chinook were released from the middle site, no group-specific estimates of survival probability are available for comparison (Models A and A' have $\hat{\phi}_i$ defined for $i=2,\dots,k-1$). The main support for the assumption is that the groups received the same treatment (same capture and handling techniques, and equal numbers and kinds of marks).

One possibility is that different times of release for the two groups caused different vulnerability to predators (day-caught fish were released at approximately 1400 and 1800, and night-caught fish at 0200 and 1600). Common Mergansers (*Mergus merganser*), mew gulls (*Larus canus*) and belted kingfishers (*Ceryle alcyon*) were common in the study area. Other predators observed included mink (*Mustela vison*), Arctic grayling (*Thymallus arcticus*), burbot (*Lota lota*), and northern pike (*Esox lucius*). A half dozen of the latter were caught about 50 m above the lower site in a large pool at the confluence of the seepage channel and the Chena (Figure 1). The only effective lures were light colored jigs resembling salmon smolts (personal observation). Some of these predators may have been more effective during either the day or night. There was, however, good cover downstream of the release sites, so released fish could presumably have found cover quickly.

If the difference in recapture rates between day and night chinook were due only to difference in survival probabilities, the difference would have been quite large. Recapture rates for day and night chinook were

$$\rho_{3d} = \phi_{d2} p_{d3} \quad \rho_{n3} = \phi_{n2} p_{n3},$$

or

$$p_{d3} = \frac{\rho_{d3}}{\phi_{d2}} \quad p_{n3} = \frac{\rho_{n3}}{\phi_{n2}}.$$

If capture probabilities were assumed equal:

$$\frac{\rho_{d3}}{\phi_{d2}} = \frac{\rho_{n3}}{\phi_{n2}}, \text{ and}$$

$$\phi_{n2} = \rho_{n3} \frac{\phi_{d2}}{\rho_{d3}}.$$

Holding the recapture rates constant at the observed levels yields

$$\phi_{n2} = 0.0098 \frac{\phi_{d2}}{0.0330}$$

allowing the following calculations:

If $\phi(d2)$ were:	$\phi(n2)$ would have been:
1.00	0.30
0.95	0.28
0.90	0.27
0.85	0.25
0.80	0.24
0.75	0.22
0.70	0.21
0.65	0.19
0.60	0.18
0.55	0.16
0.50	0.15

At the observed recapture rates, if capture probabilities were equal, the difference in ϕ 's would have been very large, from 0.67 if $\phi_{d2} = 0.95$ to 0.35 if $\phi_{d2} = 0.50$. Such large

differences in survival probability between day- and night-marked groups of fish that received equal treatment (other than time of release) seems unlikely. Therefore, at least some, if not most, of the discrepancy between p_{3d} and p_{3n} was probably due to heterogeneity in $p_{3\cdot}$.

Assuming equal ϕ 's, the level of heterogeneity at the lower site is still somewhat speculative. As calculated in the results section, if $\phi_2 = 1.00$, the estimate would be $\hat{D}_3 = 0.0232$, $SE = 0.007$. Assuming $\phi_2 = 0.95$ would not change the value much:

$$\begin{aligned}\hat{D}_3 &= \frac{p_d}{0.95} - \frac{p_n}{0.95} \\ &= \frac{0.033018}{0.95} - \frac{0.009861}{0.95} \\ &= 0.0244.\end{aligned}$$

Assuming $\phi_2 = 0.90$, heterogeneity would be $\hat{D}_3 = 0.0257$.

In conclusion, some heterogeneity probably existed at the lower site. The exact level is speculative, but was probably between 0.02 and 0.03.

The contingency table tests also seemed to indicate heterogeneity in p at the middle site, between upper site marked and unmarked fish. Upper site marked fish were 3.3% of the daytime catch at the middle site, but only 1.6% of the nighttime catch (significantly different at $P = 0.0095$).

Whether heterogeneity existed at the upper site is unknown. Also unknown is whether heterogeneity in the overall experiment was due to differences in p related to different diel behavior among subpopulations or individuals.

Reason for Robustness of N_i to Downstream Heterogeneity

In the simulations, as long as heterogeneity was confined downstream (due to timing effects, for example), abundance estimators under both Model A and Model A' (the Deaths Only Model) had low bias. With heterogeneity ranging from 0.024 to 0.144 at the lower site in Scenario A, percent relative bias (PRB) remained low ($< 2.5\%$) under both models at both the middle and upper sites (Table 9). With heterogeneity of the same range at both the lower and middle sites (Scenario B), upper site estimates, defined under Model A' only, remained essentially unbiased, but middle site estimates under either model had high bias (PRB = -23 to -44%). With heterogeneity at all three sites (a subpopulation effect) there was severe underestimation, as predicted in the literature (Carothers 1973, Cone et al. 1988, and Gilbert 1973). For example, in Simulation C1 there was -23 % PRB in \hat{N}_i under Model A' with relatively low heterogeneity ($D = 0.0244$, the observed level at the lower site assuming $\phi_2 = 0.95$).

The different behavior of the estimators to subpopulation and timing effects probably has to do with observations (Cormack 1972; Carothers 1973) that heterogeneity biases the estimate \hat{N}_i much more than \hat{M}_i (the number of marked animals in the population on occasion i , also an estimate because marked animals in an open population are subject to mortality).

Cormack (1972) illustrated subpopulation heterogeneity as follows: Animals with the "greatest catchability" will be captured and marked preferentially in the first sampling occasion. This causes unmarked animals in the next sample to have a lower average p compared to the population, and marked animals to have a higher p . In later samples, if p

still varies among individuals, the average levels of p will continue to drift in opposite directions. Consider the general CJS estimator for abundance,

$$\hat{N}_i = \frac{n_i \hat{M}_i}{m_i} ,$$

where n_i = the total number of animals captured in sample i and m_i = the number of marked animals. The statistics n_i and m_i , unrepresentatively low and high respectively, work in opposite directions to cause large underestimation in \hat{N}_i .

In contrast, the estimate for \hat{M}_i , though part of the estimator for \hat{N}_i , will contribute only small bias. The estimator for \hat{M}_i is

$$\hat{M}_i = m_i + \frac{R_i z_i}{r_i} ,$$

where R_i = the number of n_i released after the i^{th} sample; z_i = the number of animals captured before i , not captured at i , and captured again later; and r_i = the number of animals released in i (R_i) that are recaptured on later occasions. The equation can be rearranged as

$$(\hat{M}_i - m_i) / R_i = z_i / r_i .$$

On the left side of the equation, $\hat{M}_i - m_i$ can be thought of as marked fish alive but unseen in i , and R_i as marked fish seen in i . Cormack wrote that the two groups “can have had the same history of capture prior to the i th sample except that R_i contains some of the B_i new members of the population”. In other words, heterogeneity (in all occasions) tends to inflate both groups by similar amounts. Because the two groups do not change in opposite directions, the true ratio (for the population) is closely approximated. On the right side of the equation, the groups z_i and r_i have “exactly the same” relationship. The overall result, as demonstrated in computer simulations (Carothers 1973), is that heterogeneity in p causes

very small relative bias in \hat{M}_i compared to \hat{N}_i . For example, in a simulation with average $p = 0.05$, a “coefficient of variation” = 0.8 (creating a distribution of p , see above citation), $\phi = 0.8$ and $k = 3$, the average percent relative bias for $\hat{N}_3 = -39.4\%$ and for $\hat{M}_3 = -1.0\%$.

The above applies when heterogeneity occurs in all occasions. Heterogeneity confined to downstream or later occasions ($i + 1 \dots k$) does not affect the proportion $\frac{n_i}{m_i}$ in the estimator $\hat{N}_i = \frac{n_i \hat{M}_i}{m_i}$. Considering the rearranged estimator for \hat{M}_i ,

$$(\hat{M}_i - m_i) / R_i = z_i / r_i,$$

the left side of the equation (marked fish unseen in $i \div$ marked fish seen in i) is unaffected by heterogeneity in later occasions. The statistics z_i and r_i on the right side of the equation depend in part on recaptures in $i + 1 \dots k$, but as explained above, their ratio is not affected much.

Mortality is still accounted for in \hat{M}_i through the proportional comparison

$$\frac{z_i}{\hat{M}_i} = \frac{r_i}{R_i}, \text{ (Bernard and Hansen 1992; Jolly 1965 and Seber 1965) and therefore in } \hat{N}_i.$$

The simulations under Scenario A backed this up when $\phi_i = 0.95$ was accurately reflected in both the Model A and Model A' middle site estimates of \hat{N}_2 (Table 9).

The above may explain why downstream heterogeneity did not cause bias in the middle site estimate under Model A. I do not have an explanation for why downstream heterogeneity did not affect the Deaths-Only estimator:

$$\hat{N}_i = n_i + \frac{R_i z'_i}{r_i},$$

with the modified statistic

$$z'_i = z_i + \sum_{j=i+1}^k u_j .$$

Recommended 1997 Abundance Estimate

Heterogeneity likely occurred at the lower and middle sites in 1997, although the case at the upper site was unknown. If heterogeneity in p was confined to the downstream sites, and other model assumptions were adequately satisfied, the simulations suggest that the upper site Deaths Only estimate would be unbiased. It is

$$\hat{N}_1 = 133,468, (\text{SE } 12,936; \text{CI: } 108,113 - 158,823),$$

with a coefficient of variation (CV) = 0.10.

The estimate is for the number of chinook (age-1 or greater) that migrated past the upper site between May 6 and June 9. Considerable numbers of chinook migrated before and after the cut-off times, as shown by the falling capture rates at the beginning of the experiment, and the large number of chinook (627 fish) caught at the middle site during the June 10 spate (Figure 7), when the lower site screw trap was clogged and ineffective.

The above estimate still requires the assumption of equal capture probability for all chinook in the population at the upper site. Although the video showed no chinook entering the trap during the day (the observations were mostly made during a period of low day- and nighttime capture rates), probably 35% of chinook entering the trap at night during low water escaped, and schools of chinook were observed actively veering away from the mouth of the trap. Therefore, I believe that increased daytime trap evasion likely occurred during other parts of the season (probably when turbidity and discharge were moderate), in addition to lower daytime migration rates. Despite this, unless individuals or

subpopulations of chinook had propensities to migrate at different times of day, or had different abilities to avoid the trap given they were swimming past, all fish would have had an equal probability of capture at the upper site.

The Chena experiments had extremely low capture probabilities. In general, low capture probabilities and low number of sampling occasions (sites) make precise CJS estimation difficult or expensive. Even with the large sample sizes in 1997 ($n_1 = 2,299, n_2 = 2,406$ and $n_3 = 3,390$), no fish were captured on all three occasions (capture history “111”). This is not surprising, as Model A’ estimated $p_2 = 0.012$ (p was only defined for $i = 2$). Assuming a larger $p_3 = 0.020$ and perfect survival, the expected number of double recaptures would be

$$\begin{aligned} & (0.012 * 0.020) * \text{upper site releases} \\ & = 0.00024 * 2299 \\ & = 0.55, \end{aligned}$$

or less than one fish. Because the expected number was low, inserting a mock double recapture in the data did not change the abundance estimates or SE’s under any model by a single fish. (Apparently, the maximum likelihood procedure in JOLLY does not explicitly require a z statistic, but iteratively finds the combination of parameter estimates that best fit the observed data.)

Low number of capture occasions makes detection of assumption violations difficult in mark-recapture experiments, even if capture probabilities are high. For example, the Leslie test for equal capture probability among marked individuals requires at least $k = 5$ total occasions with approximately 20 individuals known to be alive and susceptible to capture on each of the three middle occasions (Begon 1979). The Component 1 Goodness of Fit test in Program JOLLY needs only $k = 3$, but requires at least two double recaptures

(history “111”; Pollock et al. 1990). The Component 2 test (Table 4) yielded a barely insignificant chi-square statistic ($\chi^2 = 3.647$, $df = 1$, $p = 0.0565$), but half of the cells were unfilled. The test was actually designed for $k = 4$ total occasions, and power must have been very low. Both components can potentially detect heterogeneity in p , with Component 2 detecting some forms of heterogeneous survival probabilities as well. Pollock et al. (1990) notes that the tests cannot detect all assumption failures, such as permanent trap-happy or trap-shy behavior, or a permanent lowering of survival due to marking. In general, low power can result from low capture or survival probabilities. Having more than 3 occasions could have allowed pooling of cells and higher power for the overall test.

The above GOF tests give no clue as to whether the assumption of equal survival between marked and unmarked fish (Appendix 1) was upheld. However, an indication of assumption violation is that the middle site Deaths Only estimate ($\hat{N}_2 = 199,303$, $SE = 31,047$) was much larger than the upper site estimate ($\hat{N}_1 = 133,468$, $SE = 12,936$), an impossibility without recruitment or immigration (neither of which were probably significant). Perhaps unequal survival between marked and unmarked fish could account for this. Unfortunately, fish were not held-over in pens for observation. Partial caudal fin clips are however a common marking method and have been used for chinook smolt in other mark-recapture experiments. The additional partial pelvic fin clips used at the middle site could have caused higher mortality, although pains were taken to make them very slight. Fish were kept in a petri dish of fresh water while marking. As noted in the methods, during inspection for marks the pelvic fins had to be lifted simultaneously with a spatula to determine which fin had been clipped. Overlooking marks could have an effect similar to higher mortality for marked fish on all occasions. However, the partial caudal fin

clips were obvious, and three of the five personnel checking for marks had experience in previous seasons, so I do not think this was a problem.

If there were subpopulation heterogeneity, based on the simulations, the upper site Deaths Only estimate would have high negative bias ($\geq 10\%$), and likely up to 30% or greater. (Simulation D1, with $D = 0.0244$, constant $\phi = 0.95$, and the “day” group 1/3rd the size of the night group, had PRB = -29% [Table 9].)

Though very speculative, a situation is imaginable that could possibly account for a subpopulation of chinook smolts having high p relative to another subpopulation during the night, and even higher relative p during the day. Chinook smolts in the Chena and in the nearby Salcha River feed during the year of their outmigration (Loftus and Lenon 1977; Daigneault 1997). Perhaps, at any one time, a portion of the population migrates slowly downstream, concentrating more on feeding during the day, while another segment of the population aggressively outmigrates (a strong urge to get to the sea having been tripped). The aggressively outmigrating segment of the population could have tended to travel during the day (instead of feeding), accounting for much higher relative p at that time. At night, p for the active outmigrants could have still been higher, but less pronounced. Smolts that quickly migrated through the study area could have had higher p than smolts that slowly fed through the study area.

Heterogeneity related to diel behavior among subpopulations of outmigrating salmon does not have a precedence in the literature. However, unequal recapture rates at downstream traps, due to inadequate mixing and diel changes in migration rates and trap evasion has been observed in salmon smolts (Bendock 1996). Without real evidence, the possible case of subpopulation heterogeneity cannot be accepted.

Recommended 1996 Estimate

The 1996 experiment had essentially the same methods and covered the same stretch of river (although the middle sites were in different locations). If heterogeneity occurred in 1996 as well, and was due only to inadequate mixing at the downstream sites, the best estimate would be

$$\hat{N}_1 = 207,423 \text{ (SE=21,547; CI: 165,191 - 249,656)}$$

under the Death's Only Model. This is different from the previous 1996 estimate (Peterson 1997), which was the average of the upper and middle site estimates under the Deaths Only Model ($\hat{N}_{\text{ave}} = 171,592$ (SE = 13,066; CI: 146,342 - 197,561)).

The estimate is for the number of chinook smolts that migrated through the upper site between May 6 and June 10, 1996.

Conclusions and Recommendations

- The abundance estimates for outmigrating chinook salmon, essentially unbiased with respect to heterogeneity due to inadequate mixing, are

1996: $\hat{N}_1 = 207,423$ (SE=21,547; CI: 165,191 - 249,656), and

1997: $\hat{N}_1 = 133,468$, (SE 12,936; CI: 108,113 - 158,823).

The estimates are for chinook that migrated past the upper site between May 6th and June 9th. They do not include chinook that migrated before and during break-up, or during the spate on June 10 - 11 (when capture rates at the inclined plane trap were high, but data could not be included because the screw trap was clogged).

- Heterogeneity probably existed at the middle and lower sites for chinook salmon in 1997. The likely cause was inadequate mixing, although a subpopulation effect was possible. Inadequate mixing alone, if confined to the lower sites, would not cause bias in the upper site estimate under the Death's Only Model. The same estimator should probably be used for the 1996 abundance estimate.
- Mixing was not achieved over the 9.4 km (5.8 miles) between the middle and lower sites, or between the 6.4 km (4.0 miles) between the upper and middle sites. For mixing, there would need to be more releases spaced over a 24 hour period, or further distances between release-recapture sites.
- The middle site inclined trap caught chinook during the day for much of the season (about 25% of the season catch at the middle site was during the day). If fish are catchable during the day, fishing all traps 24 hours per day would lessen the chances for, or magnitude of, heterogeneity in p due to inadequate mixing or "timing effects". If

24 hour fishing is not feasible, fishing all traps during the same period of high capture rates and having shorter periods between releases would probably induce the least heterogeneity.

- The relatively low daytime capture rates for chinook salmon were probably due to a combination of decreased daytime migration and increased trap evasion. The relative magnitude of each was not known and would probably vary with water conditions.
- Capture rates increased markedly with turbidity that was not necessarily accompanied with significantly higher discharge (such as from boat traffic, or from small creeks coloring the lower river just following rains, before the arrival of large volumes of water from the upper watershed). Chinook, which feed during the summer of outmigration in the Chena River (Daigneault 1997) and in the nearby Salcha River (Loftus and Lenon 1977), may follow a strategy of feeding during times of clear water, and migrating with increased turbidity when they are less susceptible to predation.
- In the video footage, 71% of age-1 or greater chinook seen passing through the mouth of the inclined plane trap were escaping. Accounting for the restricted cone of view, this represents more than 35% of chinook escaping from the trap. Other outmigrating chinook, which traveled mostly in schools, were seen swerving away from the trap to avoid entrance, or held in the cushion of slack water upstream of the 2 inch high angle aluminum forming the lip of the trap. Water velocity was not measured at the trap, but was probably between 1 and 1.5 m/s. Because tapping was done during a period of low water with generally low capture rates, chinook behavior was observed at nighttime only. However, given that chinook see better during the day, the observed evasive behaviors suggest that increased daytime trap evasion likely occurred.

- Suggested ways of improving capture efficiency of the inclined plane trap include using 25 foot Vexar (TM) screen leads and fishing in shallow, swift water (Gary Todd, Alaska Department of Fish and Game, Soldotna, personal communication), and painting the plane a drab color and shading the trap with a tarp (Troy Tydingco, MS Graduate Student, University of Alaska Fairbanks, personal communication).
- Age-0 chum and chinook salmon were not distinguishable from each other on video. None of these smaller fish (averaging approximately 40 mm compared to 70 mm for age-1 chinook) escaped from the trap during viewing. They migrated both day and night, and tended to be single or in small groups of 2 or 3. Because there were no escapes, capture rates could provide an index of their abundance. Because chum smolts are so small, partial caudal fin clips are easy to overlook and probably cause high marking mortality (Nielsen 1992, Peterson 1997).
- Significant portions of the 1997 population of outmigrating chinook were not sampled both before and after the experiment (May 6 and June 8, respectively). Chinook are outmigrating at high rates just after ice out when sampling is difficult or impossible, at least using the methods of this experiment. The 1997 season was unusual in that by far the highest capture rates of chinook were at the middle site inclined plane trap at the end of the season (336 between 2100 and 2200 on June 10, and 586 for the entire night, Appendix 2). The high rates were during high water on the night of June 10 (Figure 10). The season was characterized by low (850 to 650 cfs) discharge from May 27 through 9 June, which may have caused smolts to delay migration until heavy rains increased turbidity (on June 8) and measureable discharge (on June 10; Figures 12 and 10).

- The screw traps had higher capture rates than the inclined plane trap in both 1996 and 1997, and were probably more efficient. However, in times of high discharge, when smolt migration rates were high, heavy debris loads in the Chena clogged the screw traps, rendering them ineffective and dangerous. In contrast, the inclined plane trap was much easier and safer to clear of debris during high water, and was very effective at such times. Overall, inclined plane traps are more suited to mark-recapture of smolts in the Chena River.
- Whether the assumption of equal survival probability for all fish in the population was met is uncertain. In similar mark-recapture experiments, especially with small fish that are more susceptible to marking mortality, marked and unmarked fish should be held in pens for observation of a possible short-term marking effect on survival.
- Precise estimation of abundance and survival were hindered by low capture probabilities. This, as well as low number of capture occasions, made testing of assumptions impossible or difficult. Observed 1996 and 1997 sample sizes, effort, and capture probabilities should be used in the design of any future mark-recapture studies of smolt in the Chena to check attainable levels of precision and test power (of assumption and between-model tests).

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Appendix 1: CJS Methodology

The CJS Model yields estimates of abundance and survival for populations open to births, deaths or permanent migration. Births and deaths are not separable from migration without additional information. At least three capture occasions (or in this study, sites) are required ($i = 1, 2, \dots, k; k \geq 3$). Animals are captured, marked and released on the first occasion. On subsequent occasions, marked and unmarked animals receive an additional, occasion-specific mark, except for the final occasion, when animals are inspected for the presence of marks only. Capture history data is recorded as a “1” or a “0” for each occasion, capture symbolized as “1” and not captured as a “0”. For example, “101” would represent captured on the first occasion, not captured on the second occasion, and recaptured on the third occasion.

The CJS statistics (Pollock et al. 1990) are:

- m_i = the number of marked animals caught in the sample,
- u_i = the number of unmarked animals captured in this sample,
- n_i = the total number of animals captured in the sample ($m_i + u_i$),
- R_i = the number if n_i released after the sample is taken (sometimes less than n_i if losses occur),
- r_i = the number of R_i animals released that are captured again later, and
- \tilde{z}_i = the number of animals captured before this sample site and captured again later, but not captured at this sample site.

The following parameters can then be estimated:

- M_i = the number of marked animals in the population at the time the i th sample is

taken,

N_i = the total number of animals in the population at the time the i th sample is taken,

B_i The total number of new animals entering the population between the i th and the $(i + 1)$ th sample is taken,

ϕ_i = the survival probability for all animals between the i th and $(i + 1)$ th sample, and

p_i = the capture probability for all animals in the i th sample.

Some of the above parameters are useful only in that they allow estimation of other parameters of biological interest. The general estimators and the occasions for which they are defined are:

$$\hat{M}_i = m_i + \frac{R_i z_i}{r_i}, \text{ defined for } i=2, \dots, k-1;$$

$$\hat{N}_i = \frac{n_i \hat{M}_i}{m_i}, \text{ } i=2, \dots, k-1;$$

$$\hat{\phi}_i = \frac{\hat{M}_{i+1}}{\hat{M}_i - m_i + R_i}, \text{ } i=1, \dots, k-2;$$

$$\hat{B}_i = \hat{N}_{i+1} - \hat{\phi}_i (\hat{N}_i - n_i + R_i), \text{ } i=2, \dots, k-2;$$

and

$$\hat{p}_i = \frac{m_i}{\hat{M}_i} = \frac{n_i}{\hat{N}_i}, \text{ } i=2, \dots, k-1;$$

The above estimators under the general CJS model (Model A) can be simplified to allow deaths only (Model A'). The simplification gives the Deaths Only Model greater precision and allows for an additional abundance estimate. Model A' estimators are:

$$\hat{N}_i = n_i + \frac{R_i z'_i}{r_i}, \text{ } i=1, 2, \dots, k-1;$$

and

$$\hat{\phi}_i = \frac{\hat{N}_{i+1}}{\hat{N}_i - n_i + R_i}, \quad i=1,2,\dots,k-2.$$

The modified statistic z' is

$$z'_i = z_i + \sum_{j=i+1}^k u_j.$$

The variance formulas for the above estimators are complex and shown in Pollock et al. (1990).

The statistic z_i allows for estimation of the number of marked animals in the population (\hat{M}_i), an unknown because of death, birth and migration. The estimate \hat{M}_i is required for all of the above open population estimators. The statistic z_i , and therefore the CJS Model, requires at least 3 occasions.

The estimators shown above are in closed form (they have a single solution solvable by hand). However, a computer program such as JOLLY is required to iteratively fit the most likely solution (out of many) to the data and get maximum likelihood estimates (Pollock et al 1990).

The model assumptions from Pollock et al. (1990) are:

1. Every animal in present in the population at the time of the i th sample ($i = 1, 2, \dots, k$) has the same probability of capture (p_i).
2. Every animal present in the population immediately after the i th sample has the same probability of survival (ϕ_i) until the $(i+1)$ th sampling time ($i = 1, 2, \dots, k-1$).
3. Marks are not lost or overlooked.
4. All samples are instantaneous and each release is made immediately after the sample.

Appendix 2: Unsummarized 1997 data for capture, fish length, temperature, turbidity, and video footage.

Upper Site Capture Data - Chinook, 1997				
Date	Period	Captured	Released (marked)	Notes:
5/06/97	2000-0000	14	14	
"	0000-0300	44	44	
"	0300-0800	40	40	
5/07/97	2000-2300	12	12	
"	2300-0200	17	17	
"	0230-0700	70	70	
5/08/97	2000-2300	54	53	trap kill
"	2300-0245	31	31	
"	0245-0730	61	59	trap kill
5/09/97	1900-2200	93	93	
"	2200-0100	67	67	
"	0100-0600	39	39	
5/10/97 ¹	1900-2200	-	-	¹ No data. Falling water level
"	2200-0100	-	-	grounded screw trap. Had difficulty
"	0100-0500	-	-	moving 20 m upstream to deeper water.
5/11/97	1900-2200	60	59	trap kill
"	2200-0100	29	29	
"	0100-0600	24	24	
5/12/97	1900-2200	34	33	trap kill
"	2200-0100	72	72	
"	0100-0600	69	68	
5/13/97	1900-2200	21	17	4 trap kill or injured, likely from log
"	2200-0100	72	72	that jammed trap.
"	0100-0600	77	77	
5/14/97	0900-1300	17	16	trap kill
"	1300-1700	16	16	
"	1900-2200	33	33	
"	2200-0100	59	58	trap kill
"	0100-0600	21	19	trap kill
5/15/97	1900-2200	21	20	trap kill
"	2200-0100	50	48	trap kill
"	0100-0600	13	10	2 killed by trap, 1 not recovered
5/16/97	1900-2200	22	16	trap kill
"	2200-0100	55	52	trap kill
"	0100-0600	14	11	trap kill
5/17/97	1900-2200	21	21	
"	2200-0100	43	42	trap kill
"	0100-0600	44	43	trap kill
5/18/97	1900-2200	25	24	trap kill
"	2200-0100	54	54	
"	0100-0700	25	25	
5/19/97	1900-2200	33	33	
"	2200-0100	42	42	
"	0100-0700	52	51	injured and not released
5/20/97	1900-2200	24	24	
"	2200-0100	58	58	
"	0100-0700	49	49	

5/21/97	1900-2200	17	17	
"	2200-0100	44	44	
"	0100-0700	37	37	
5/22/97	1900-2200	8	8	
"	2200-0100	55	55	
"	0100-0700	35	35	
5/23/97	1900-2200	21	21	
"	2200-0100	34	34	
"	0100-0700	30	30	
5/24/97	1900-2200	24	24	
"	2200-0100	74	74	
"	0100-0800	12	12	
5/25/97	1900-2200	23	23	
"	2200-0100	19	19	
"	0100-0800	35	35	
5/26/97	1900-2200	6	6	
"	2200-0100	9	9	
"	0100-0800	5	5	
5/27/97	900-1300	0	0	
"	1300-1700	0	0	
"	1900-2200	1	1	
"	2200-0100	5	5	
"	0100-0700	5	5	
5/28/97	1900-2200	0	0	
"	2200-0100	0	0	
"	0100-0800	4	4	
5/29/97	1900-2200	1	1	
"	2200-0100	3	3	
"	0100-0800	5	5	
5/30/97	1900-0100	0	0	
"	0100-0700	6	1	
5/31/97	1900-0100	10	10	
"	0100-0700	10	10	
6/01/97	1900-0100	5	5	
"	0100-0700	1	1	
6/02/97	1900-0100	0	0	
"	0100-0700	0	0	
6/03/97	1900-0100	1	1	
"	0100-0700	2	2	
6/04/97	1900-0700	1	1	
6/05/97	1900-0700	4	4	
6/06/97	1900-0700	0	0	
6/07/97	0700-1700	2	2	
"	1700-0700	0	0	
6/08/97	0700-1900	0	0	
"	1900-1700	0	0	
6/09/97 ³	0700-1900	1	0	³ 6/9 and 6/10 discluded from totals
"	1900-0700	35	35	(not enough time for fish to reach
6/10/97	0700-1900	5	5	downstream sites before season end).
Upper Site Totals		captured	released	
(discluding shaded area)		2345	2304	

Middle Site Capture/Release Data - Chinook, 97								
(UC = partial upper caudal clip, LC = lower caudal, PFC = pelvic fin clip)								
Date	Period	Unmarked	Upper Caudal	Releases LC+:		Releases, UC/LC+:		Notes
		Captures	Captures	PFC-Left	PFC-Right	PFC-Left	PFC-Right	
5/09/97	0900-1300	16	1	16		1		
"	1300-1700	34	0	34				
"	2100-0100 ¹	60	2		28			¹ 34 killed, including
"	0100-0500	10	2		10			2 2 recaps. Bucket had
5/10/97	0900-1300	9	0	9				detergent residue from
"	1300-1700	5	0	5				previous year in it.
"	2100-0100	59	1		59		1	
5/11/97	0900-1300	5	0	5				
"	1300-1700	4	0	4				
"	2100-0100	9	0		8			1 caught on ramp and injured
"	0100-0500	26	2		26		2	
5/12/97	0900-1300	2	0	2				
"	1300-1700	1	0	1				
"	2100-0100	12	0		12			
"	0100-0500	28	0		28			
5/13/97	0900-1300	5	0	5	0			
"	1300-1700	8	0	8	0			
"	2100-0100	54	2		54		2	
"	0100-0500	69	0		69			
5/14/97	0900-1300	5	1	5		1		
"	1300-1700	5	0	5				
"	2100-0100	62	3		62		3	
"	0100-0500	20	0		20			
5/15/97	0900-1300	22	0	22				
"	1300-1700	123	1	116		1		7 did not recover
"	2100-0100	40	1		40			UC killed by trap
"	0100-0500	79	0		79			
5/16/97	0900-1300	6	0	6				
"	1300-1700	0	0					
"	2100-0100	116	1		116		1	
"	0100-0500	34	0		34			
5/17/97	0900-1700	74	0	74				

"	2100-0100	24	0		24				
"	0100-0500	17	0		17				
5/18/97	0900-1300	24	0	24					
"	1300-1700	47	1	47		1			
"	2100-0100	39	0		39				
"	0100-0500	31	1		31			1	
5/19/97	0900-1300	4	0	4					
"	1300-1700	22	2	22		2			
"	2100-0100	35	0		35				
"	0100-0500	21	0		21				
5/20/97	900-1700	13	0	13					
"	2100-0500	84	1		84			1	
5/21/97	0900-1700	3	0	3					
"	2100-0500	11	1		11			1	
5/22/97	0900-1700	2	0	2					
"	2100-0500	2	0		2				
5/23/97	0900-1700	0	0						
"	2100-0500	13	0		13				
5/24/97	0900-1700	39	3	39		3			
"	2100-0500	239	10		239			10	
5/25/97	0900-1700	96	10	96		10			
"	2100-0500	82	1		82			1	
5/26/97	0900-1700	9	1	9		1			
"	2100-0500	12	0		12				
5/27/97	0900-1700	1	0	1					
"	2100-0500	1	0		1				
5/28/97	0900-1700	0	0						
"	2100-0500	5	0		5				
5/29/97	0900-1700	1	0	1					
"	2100-0500	0	0						
5/30/97	0900-1700	0	0						
"	2100-0500	1	0		1				
5/31/97	0900-1700	1	0	1					
"	2100-0500	12	0		12				
6/01/97	0900-1700	2	0	2					
"	2100-0500	17	1		17			1	
6/02/97	0900-1700	1	0	1					

"	2100-0500	4	0		4			
6/03/97	0900-1700	6	0	6				
"	2100-0500	0	0					
6/04/97	0900-1700	2	0	1				1 unmarked dead on arrival
"	2100-0500	0	0					
6/05/97	0900-1700	36	0	36				
"	2100-0500	28	0		28			
6/06/97	0900-1700	-	-	-	-	-	-	- Unable to set trap (no data)
"	2100-0500	12	0		12			
6/07/97	0900-1700	0	0					
"	2100-0500	17	0		17			
6/08/97	0900-1700	0	0					
"	2100-0500	262	0		262			
6/09/97	0900-1700	11	0	11				
"	2100-0500	110	0		110	0		
6/10/97	0900-1700 ^{2,3}	39	2	39		2		² Not enough time for releases on 6/10 and 6/11 to reach lower site, so they were not included in totals.
"	2100-2200 ⁴	336	0		88			
"	0100-0200	127	0		50			
"	0300-0400	77	0		50			
"	0500-0600	46	0		46			³ Water silting up, not rising.
6/11/97	0915-1015	23	0					⁴ Water rising quickly, had to raise trap and get help working up catch.
"	1100-1200	32	0					
"	1300-1400	30	0					
Middle Site Totals (discluding shaded area)		Unmarked Captures	UC captures	Releases LC+:		Releases, UC/LC+:		
				PFC-left	PFC-right	PFC-left	PFC-right	
		2440	51	636	1724	20	26	

Lower Site Recapture Data - Chinook, 1997. Gray area not included in totals. (UC = partial upper caudal clip, LC = lower caudal clip, PFC = pelvic fin clip)						
Date	Period	Unmarked Captures	UC Captures	LC+:		Notes
				PFC-Left	PFC-Right	
5/06/97 ¹	2000-0000	134	0			'5/6, 5/7 and 5/8 not counted in totals (not enough time for arrival of marked fish from upstream sites).
5/07/97	2000-2300	261	0			
"	2330-0230	120	0			
"	0230-0630	84	0			
5/08/97	1900-2200	73	0			
"	2200-0100	222	0			
"	0100-0500	88	0			
5/09/97	1900-2200	162	1			
"	2200-0100	72	1			
"	0100-0500	134	1			
5/10/97	1900-2200	95	1	1		
"	2200-0100	83	0			
"	0100-0500	114	2			
5/11/97	1900-2200	50	1			
"	2200-0100	72	0			
"	0100-0500	42	0			
5/12/97	1900-2200	21	0			
"	2200-0100	58	1			
"	0100-0500	55	1			
5/13/97	1900-2200	14	1			
"	2200-0100	50	1	2		
"	0100-0500	101	3			
5/14/97	0900-1300	23	0			
"	1300-1700	15	0			
"	1900-2200	17	2			
"	2200-0100	67	4		1	
"	0100-0500	73	0		2	
5/15/97	1900-2200	146	3		2	
"	2200-0800	46	0	1		
5/16/97	1900-2200	78	2			
"	2200-0100	191	1		3	
"	0100-0800	85	1			
5/17/97	1900-2200	16	0	1		

"	2200-0100	137	0	3	1		
"	0100-0600	40	0	1	1		
5/18/97	1900-2200	42	0		1		
"	2200-0100	245	1	2			
"	0100-0700	58	0	2	1		
5/19/97	1900-2200	35	0	1			
"	2200-0100	64	1		2		
"	0100-0600	71	1	1			
5/20/97	1900-2200	16	0	1			
"	2200-0100	54	2	1	1		
"	0100-0600	75	4				
5/21/97	1900-2200	14	0		1		
"	2200-0100	33	2				
"	0100-0600	42	1	1			
5/22/97	1900-2200	9	1				
"	2200-0100	15	1				
"	0100-0600	37	1				
5/23/97	1900-2200	7	0				
"	2200-0100	11	1			UC had PFC-rt (timing experiment)	
"	0100-0800	60	1	1		UC had PFC-rt (timing experiment)	
5/24/97	1900-2200	10	1				
"	2200-0100	11	0				
"	0100-0800	28	1	1			
5/25/97	1900-2200	7	0				
"	2200-0100	8	2	1			
"	0100-0800	15	0				
5/26/97	1900-2200	1	0				
"	2200-0100	1	0				
"	0100-0800	3	0				
5/27/97	900-1300	0	0				
"	1300-1700	1	0				
"	1900-2200	0	0		1		
"	2200-0100	1	0				
"	0100-0700	1	0				
5/28/97	1900-2200	0	0				
"	2200-0100	0	0				
"	0100-0700	0	0				
5/29/97	1900-2200	0	0				
"	2200-0100	1	0				

"	0100-0700	0	0					
5/30/97	1900-0100	0	0					
"	0100-0700	1	0					
5/31/97	1900-0100	1	0					
"	0100-0700	1	0					
6/01/97	1900-0100	0	0					
"	0100-0700	0	0					
6/02/97	1900-0100	1	0					
"	0100-0700	0	0					
6/03/97	1900-0100	0	0					
"	0100-0700	0	0					
6/04/97	1900-0700	0	0					
6/05/97	1900-0700	0	0					
6/06/97	1900-0700	0	0					
6/07/97	1900-0700	0	0					
6/08/97	0700-0700	0	0					
6/09/97	1900-0700	0	0					
6/10/97	0700-1900	2	0					
"	1900-2330	106	0					
"	2330-0130 ²	134	0					
6/11/97	0900-1000	24	0					
Lower Site Totals		unmarked caps	UC caps	LC +:				
(discluding captures				pfc left	pfc right			
before 5/9)		3303	48	21	17			

²Trapping stopped for night (very heavy debris load clogged screw trap)

Capture Data, Upper Site Chum, 1997					
Date	Period	Captured	Released	Notes	
5/06/97	2000-0000	8	8		
"	0000-0300	17	17		
"	0300-0800	52	51		
5/07/97	2000-2300	8	8		
"	2300-0200	17	17		
"	0230-0700	50	49		
5/08/97	2000-2300	28	28		
"	2300-0245	2	1		
"	0245-0730	22	22		
5/09/97	1900-2200	27	26		
"	2200-0100	1	1		
"	0100-0600	7	7		
5/10/97	¹ 1900-2200	-	-	- ¹ No data. Falling water level caused screw trap to hit bottom and had difficulties moving it slightly upstream to deeper location.	
"	2200-0100	-	-		
"	0100-0500	-	-		
5/11/97	1900-2200	4	4		
"	2200-0100	10	10		
"	0100-0600	15	14		
5/12/97	1900-2200	29	29		
"	2200-0100	16	16		
"	0100-0600	14	14		
5/13/97	1900-2200	15	11		
"	2200-0100	9	9		
"	0100-0600	18	18		
5/14/97*	0900-1300	41	40		
"	1300-1700	11	9		
"	1900-2200	19	18		
"	2200-0100	10	10		
"	0100-0500	4	4		
"	0500-0900	0	0		
5/15/97	1900-2200	2	1		
"	2200-0100	1	1		
"	0100-0600	0	0		
5/16/97	1900-2200	3	1		
"	2200-0100	0	0		
"	0100-0600	8	8		
5/17/97	1900-2200	5	5		

"	2200-0100	0	0			
"	0100-0600	4	4			
5/18/97	1900-2200	3	3			
"	2200-0100	0	0			
"	0100-0700	3	3			
5/19/97	1900-2200	2	2			
"	2200-0100	0	0			
"	0100-0700	2	2			
5/20/97	1900-2200	2	2			
"	2200-0100	1	1			
"	0100-0700	6	6			
5/21/97	1900-2200	3	3			
"	2200-0100	3	3			
"	0100-0700	1	1			
5/22/97	1900-2200	0	0			
"	2200-0100	0	0			
"	0100-0700	2	2			
5/23/97	1900-2200	3	3			
"	2200-0100	2	2			
"	0100-0700	3	3			
5/24/97	1900-2200	0	0			
"	2200-0100	7	7			
"	0100-0800	4	4			
5/25/97	1900-2200	5	5			
"	2200-0100	9	9			
"	0100-0800	3	3			
5/26/97	1900-2200	9	9			
"	2200-0100	4	4			
"	0100-0800	15	15			
5/27/97	900-1300	1	1			
"	1300-1700	2	2			
"	1900-2200	1	1			
"	2200-0100	0	0			
"	0100-0700	4	4			
5/28/97	1900-2200	0	0			
"	2200-0100	0	0			
"	0100-0800	1	1			
5/29/97	1900-2200	2	1			
"	2200-0100	0	0			
"	0100-0800	2	2			
5/30/97	1900-0100	0	0			

"	0100-0700	1	0			
5/31/97	1900-0100	3	3			
"	0100-0700	0	0			
6/01/97	1900-0100	2	1			
"	0100-0700	0	0			
6/02/97	1900-0100	0	0			
"	0100-0700	0	0			
6/03/97	1900-0100	2	2			
"	0100-0700	1	1			
6/04/97	1900-0700	1	1			
6/05/97	1900-0700	0	0			
6/06/97	1900-0700	0	0			
6/07/97	0700-1700	0	0			
"	1700-0700	0	0			
6/08/97	0700-1900	3	3			
"	1900-1700	0	0			
6/09/97	0700-1900	0	0			
"	1900-0700	0	0			
6/10/97	0700-1900	4	4			
U.S. Total Chum:		captured	released			
		599	580			

Lower Site Capture Data - Chum, 1997					
Date	Period	Unmarked	UC	LC	Notes
5/06/97	2000-0000	12		0	
5/07/97	2000-2300	24			
"	2330-0230	8			
"	0230-0630	12			
5/08/97	1900-2200	3			
"	2200-0100	10			
"	0100-0500	20			
5/09/97	1900-2200	35			
"	2200-0100	8			
"	0100-0500	18			
5/10/97	1900-2200	12			
"	2200-0100	11			
"	0100-0500	42			
5/11/97	1900-2200	9			
"	2200-0100	20			
"	0100-0500	31			
5/12/97	1900-2200	15			
"	2200-0100	13			
"	0100-0500	17			
5/13/97	1900-2200	24			
"	2200-0100	15			
"	0100-0500	33			
5/14/97	0900-1300	14			
"	1300-1700	40			
"	1900-2200	17			
"	2200-0100	24			
"	0100-0500	15			
5/15/97	1900-2200	50			
"	2200-0800	8			
5/16/97	1900-2200	25			
"	2200-0100	4			
"	0100-0800	34			
5/17/97	1900-2200	27			
"	2200-0100	7			
"	0100-0600	2			
5/18/97	1900-2200	11			
"	2200-0100	2			
"	0100-0700	12			
5/19/97	1900-2200	9			
"	2200-0100	10			
"	0100-0600	4			
5/20/97	1900-2200	5			
"	2200-0100	3			
"	0100-0600	10			
5/21/97	1900-2200	3			
"	2200-0100	2			
"	0100-0600	1			

5/22/97	1900-2200	1				
"	2200-0100	1				
"	0100-0600	6				
5/23/97	1900-2200	2				
"	2200-0100	1				
"	0100-0800	11				
5/24/97	1900-2200	5				
"	2200-0100	10				
"	0100-0800	20				
5/25/97	1900-2200	6				
"	2200-0100	21				
"	0100-0800	11				
5/26/97	1900-2200	5				
"	2200-0100	1				
"	0100-0800	3				
5/27/97	900-1300	1				
"	1300-1700	4				
"	1900-2200	0				
"	2200-0100	2				
"	0100-0700	1				
5/28/97	1900-2200	1				
"	2200-0100	0				
"	0100-0700	0				
5/29/97	1900-2200	0				
"	2200-0100	0				
"	0100-0700	0				
5/30/97	1900-0100	0				
"	0100-0700	0				
5/31/97	1900-0100	7				
"	0100-0700	2				
6/01/97	1900-0100	3				
"	0100-0700	2				
6/02/97	1900-0100	0				
"	0100-0700	2				
6/03/97	1900-0100	0				
"	0100-0700	1				
6/04/97	1900-0700	0				
6/05/97	1900-0700	0				
6/06/97	1900-0700	0				
6/07/97	1900-0700					
6/08/97	0700-0700					
6/09/97	0700-1900	4				
6/10/97	0700-1900	0				
"	1900-2330	0				
"	¹ 2330-0130	0				¹ Trapping stopped. Heavy debris load clogging trap.
6/11/97	0900-1000	0				
L.S. Chum:		unmarked	uc	lc		
		865	0	0		

Table . Middle Site Length Data (Day and Night) - Chinook, 1997				
Date	Day		Night	
	Number Measured	Average Length (mm)	Number Measured	Average Length (mm)
5/09/97	60	75	83	75
5/10/97	17	77	0	N.A.
5/11/97	9	75	0	N.A.
5/12/97	3	81	0	N.A.
5/13/97	13	74	0	N.A.
5/14/97	14	73	0	N.A.
5/15/97	45	76	0	N.A.
5/16/97	6	77	0	N.A.
5/17/97	30	77	0	N.A.
5/18/97	41	76	0	N.A.
5/19/97	28	77	0	N.A.
5/20/97	13	78	0	N.A.
5/21/97	3	76	0	N.A.
5/22/97	2	77	0	N.A.
5/23/97	0	N.A.	0	N.A.
5/24/97	29	76	0	N.A.
5/25/97	30	73	0	N.A.
5/26/97	10	75	0	N.A.
5/27/97	1	81	0	N.A.
5/28/97	0	N.A.	4	82
5/29/97	1	75	0	N.A.
5/30/97	0	N.A.	0	N.A.
5/31/97	1	100	11	77
6/01/97	2	84	18	80
6/02/97	1	72	4	80
6/03/97	6	80	0	N.A.
6/04/97	1	79	5	81
6/05/97	35	82	27	79
6/06/97	0	N.A.	12	82
6/07/97	0	N.A.	22	83
6/08/97	0	N.A.	42	82
6/09/97	0	N.A.	33	80
6/10/97	30	84	33	81
6/11/97	0	N.A.	0	N.A.

Middle Site Temperature and Turbidity Data, 1997				
Date	Period	Temperature	Turbidity (¹ 100 PPM silica-equivalent)	Notes
5/09/97	0900-1300	-		¹ US Geological Survey standard using the platinum- wire method
"	1300-1700	-		
"	2100-0100	3	25	
"	0100-0500	3		
5/10/97	0900-1300	5		
"	1300-1700	6	20	
"	2100-0100	5		
5/11/97	0900-1300	6		
"	1300-1700	6	18	
"	2100-0100	5		
"	0100-0500	5		
5/12/97	0900-1300	6		
"	1300-1700	6	15	
"	2100-0100	5		
"	0100-0500	5		
5/13/97	0900-1300	6		
"	1300-1700	6	17	
"	2100-0100	5		
"	0100-0500	5		
5/14/97	0900-1300	5		
"	1300-1700	6	30	
"	2100-0100	5		
"	0100-0500	5		
5/15/97	0900-1300	5		
"	1300-1700	5	24	
"	2100-0100	4		
"	0100-0500	4		
5/16/97	0900-1300	6		
"	1300-1700	5	17	
"	2100-0100	5		
"	0100-0500	5		
5/17/97	0800-1700	5		
"	2100-0100	5	-	
"	0115-0530	5		
5/18/97	0900-1300	5		
"	1300-1700	5	20	
"	2100-0100	5		

"	0100-0500	4		
5/19/97	0900-1300	6		
"	1300-1700	7	15	
"	2100-0100	7		
"	0100-0500	6		
5/20/97	900-1700	8	9	
"	2100-0500	8		
5/21/97	0900-1700	8	8	
"	2100-0500	7		
5/22/97	0900-1700	8	8	
"	2100-0500	7		
5/23/97	0900-1700	7	≤7	
"	2100-0500	6		
5/24/97	0900-1700	6	≤7 ²	² Turbidity was ≤ 7ppm AM
"	2100-0500	6		and 11 ppm by afternoon
5/25/97	0900-1700	10	≤7 ²	(Memorial Day boat traffic)
"	2100-0500	7		
5/26/97	0900-1700	9	≤7 ³	³ Turbidity was ≤ 7ppm AM
"	2100-0500	8		and 13ppm by afternoon
5/27/97	0900-1700	9	≤7	
"	2100-0500	10		
5/28/97	0900-1700	11	≤7	
"	2100-0500	9		
5/29/97	0900-1700	10	≤7	
"	2100-0500	9		
5/30/97	0900-1700	9	≤7	
"	2100-0500	9		
5/31/97	0900-1700	8	≤7	
"	2100-0500	7		
6/01/97	0900-1700	8	≤7	
"	2100-0500	8		
6/02/97	0900-1700	9	≤7	
"	2100-0500	8		
6/03/97	0900-1700	9	≤7	
"	2100-0500	8		
6/04/97	0900-1700	12	≤7	
"	2100-0500	11		
6/05/97	0900-1700	13	≤7	
"	2100-0500	12		
6/06/97	0900-1700	-	≤7	
"	2100-0500	14		
6/07/97	0900-1700	12	≤7	

"	2100-0500	11			
6/08/97	0900-1700	14	≤7		
"	2100-0500	11			
6/09/97	0900-1700 ⁴	11	12	⁴ water not rising	
"	2100-0500	9	21		
6/10/97	0900-1700 ⁵	9	35	⁵ water rising afternoon	
"	2100-2200 ⁶	9		⁶ water rising very rapidly	
"	0100-0200	8			
"	0300-0400	7			
"	0500-0600	7			
6/11/97	0915-1015	7	60		
"	1100-1200	8			
"	1300-1400	8			

Video data from the middle site inclined plane trap, Chena River, 1997. Elevation above the river bottom was triangulated using the apparent elevation fish swam past the sighting board and distance, estimated to within one foot by comparing fish to corrugations in the ramp bottom. Note that chums were indistinguishable from age-0 chinook.								
Time	Chinook in out		Sighting Board Reading (inches)	Distance (1, 2, 3, or 4 feet)	Calculated Elevation Above River Bottom (inches)	Chums or Age-0 Chinook	Other Species	Notes
Tape: 5/31 1530 - 1707								
15:30:23						1		
15:30:34						1		
15:33:45						4		
15:40:34						10		
16:20:59						2		
16:22:03						2		
16:23:51						1		
16:33:28						1		
16:53:26						1		
17:00:04						1		
17:07:00								End of Tape.
Total	0	0				24		
Tape: 5/31 2130 - 2219								
22:11:45						2		
22:15:02						4		
22:22:53						1		
22:29:21						2		
22:48:35						1		
22:49:21						1		
23:19:45								End of tape.

Total		0	0				11			
Tape: 6/02 1200 - 1302										
12:22:21	¹							Lamprey	¹ Very close, clear view.	
13:02:35									End of tape.	
Total		0	0				0			
Tape: 6/03 0215 - 0405										
04:05:28									Nothing, end of tape.	
Total		0	0				0			
Tape: 6/05 0145 - 0248										
01:58:30							1			
02:00:18	²	2	2	12	4	13			² Rest of school, about 16 chinook, just missed trap; escapes just above lip.	
02:00:38			1			2				
02:17:24								lamprey		
02:24:42	³								³ School of five chinook barely avoided trap.	
02:26:48							1			
02:37:57							1			
02:48:15									End of tape.	
Total		2	3				3			
Tape: 6/05, 1998, 1230 - 1332										
12:44:32							1			
12:54:21								sculpin		
12:59:31							1			
13:00:41								whitefish	Round whitefish, excellent view.	
13:08:11							1			
13:32:00									End of Tape.	
Total		0	0				3			
Tape: 6/05 2100 - 2232										
21:22:24							1			
21:31:51							3			

21:35:58						1		
22:27:08	⁴							⁴ Large school of chums/age-0's misses trap.
22:31:31								End of tape.
Total		0	0			5		
Tape: 6/7 2220 - 2324								
22:21:37	⁵							⁵ School (~20) chinook or chum (too distant
22:23:45	⁶							to tell) swim past.
22:23:48	⁷	3	3	4	3	5		⁶ Another large school chinook misses trap.
22:23:59		1		4	1	2		⁷ Chinook enter, but immediately escape.
22:27:18						1		
22:31:32						1		
22:37:40	⁸							⁸ Near miss, large school of chinook.
22:38:26	⁹							⁹ Another near miss, large school of chinook.
22:49:07								" " "
22:50:01	¹⁰							¹⁰ Large chinook school turns and avoids trap.
23:02:10						1		
23:04:54	¹¹	3		14	4	14		¹¹ All but three of large school miss trap.
23:05:03			1	2	4	4		
23:08:16	¹²							¹² Near miss, large school of chinook.
23:11:47	¹³							¹³ " " "
23:11:50	¹⁴	4		18	3	14		¹⁴ School of age-0's or chums with several
23:12:12			3	2	4	4		chinook mixed in.
23:23:44								End of Tape.
Total		11	7			3		
Tape: 6/08 0900 - 1000								
09:21:22						2		
09:24:22						3		
09:52:52							Lamprey	
10:00:00								End of tape.

Total	0	0				5		
Tape: June 9, 1998, 0025 - 0132								
00:30:56		1	24	3	18			
00:31:29						1		
00:35:40	13		18	2	10			
00:35:59		16	2	1	2			
00:36:52	2		2	1	2			
00:37:03		1	2	1	2			
00:37:11		8	2	2	3			
00:37:21		1	2	1	2			
00:42:08	19		20	3	15			
00:42:10	4		2	3	3			
00:42:13		1	2	1	2			
00:42:35		4	2	1	2			
00:43:18	6		16	4	16			
00:43:31		1	2	1	2			
00:44:04						1		
00:44:08	14		16	3	13			
00:44:16						1		
00:44:18		2	2	1	2			
00:44:28		1	2	1	2			
00:45:35	¹⁵							¹⁵ Several chinook holding on river
00:49:02						1		bottom 5 - 10 cm in front of trap lip.
00:49:05						1		Chinook remained visible there
00:49:54		1	2	4	4			until the end of the tape. Probably not the
00:49:59		1	2	1	2			same fish entire time, but rate at which
00:50:58	17		24	2	13			replaced by other drifting fish unknown

00:51:00	8	2	8	2	6			(on edge of view).	
00:51:05		1	2	1	2				
00:51:07		1	2	4	4				
00:51:09		2	2	4	4				
00:51:12		2	2	4	4				
00:51:16		3	2	4	4				
00:51:24		4	2	2	3				
00:53:58						18			
01:02:22	1		22	2	12				
01:02:23	1		10	2	6				
01:02:24	1		8	2	6				
01:02:25		2	2	1	2				
01:02:34		1	2	4	4				
01:02:41		3	2	1	2				
01:03:00		1	2	1	2				
01:05:20	6		24	3	18				
01:05:38		12	2	2	3				
01:06:26	1		20	2	11				
01:07:03	1		4	2	4				
01:08:41						1			
01:13:18	4		26	3	19				
01:15:45		1	4	1	3				
01:17:58		1	2	1	2				
01:19:44	4		26	2	14				
01:19:46	1	1	6	3	6				
01:24:09						1			
01:26:41	5		20	2	11				
01:27:00		1	2	2	3			End of Tape.	
Total	108	76				25			

Tape: 6/09 2100 - 2200									
21:00:02	¹⁶					1		¹⁶ School, ~ 30 age-0s or chums miss trap	
21:10:01	¹⁷	1		12	2	7	2	(except for one).	
21:11:26								¹⁷ 1 chinook and 2 "chum" apparently	
21:11:33	¹⁸		1	6	1	3		travelling together.	
21:12:22							1	¹⁸ Struggling on edge of camera view	
21:18:37							1	(counted as escaped).	
21:22:50							4		
21:23:35							1		
21:23:36							1		
21:25:45							1		
21:25:49	¹⁹							¹⁹ School of "chums" or chinook passed by	
21:27:37							1	(too distant to tell which).	
21:45:40							2		
22:00:00								End of tape.	
Total		1	1				15		
Tape: 6/10 0300 - 0400									
<<Cannot see, too much turbidity >>									

Appendix 3: Details of using PROC SIMULATE

Program RELEASE uses the CJS Model, but for survival estimation only, and usually for animals that are conditioned upon release (Burnham et al. 1987). For example, the survival rate for a known population of treatment fish released above a dam would be estimated and compared to the survival rate for a similar, known number of control fish released below the dam. A method was needed to get PROC SIMULATE of Program RELEASE to simulate capture history data (1's and 0's) for the Chena River CJS and heterogeneity experiment.

To simulate the true, unknown population of chinook arriving at the Chena upper site, a number of fish equal to the chosen population size was therefore “released” in PROC SIMULATE from an imaginary site upstream of the Chena “upper site”. For example, in the input in Table 10, initial population size is specified in the second line from the bottom as “R(1) = 82500 82500”. Equal subpopulations of “Day” and “Night” fish with a total population size of 165,000 therefore pass through the upper site during the season. So that the population does not decrease between the imaginary release site and the “upper site”, survival rates are perfect for the first interval (“phi(1) = 1.0 1.0”). The additional, imaginary release site causes occasion $i = 1$ in the Chena experiment to read as occasion $i = 2$ in the input. For example, “phi(2)” represents survival in the first occasion in the Chena experiment (between the upper and middle sites), and so-on for the other parameters. In this simulation, only the lower site capture probabilities (p_3 's) are different to simulate

Table 10. Example input for PROC SIMULATE.

```

PROC TITLE A1.inp;
PROC SIMULATE OCCASIONS=4 GROUPS=2 NSIM=1000 SEED=7654321 EXPECT;
GLABEL(1)=Day;
GLABEL(2)=Night;
phi(1)=1.0      1.0;
phi(2)=0.95     0.95;
phi(3)=0.95     0.95;
p(2)=0.0149474 0.0149474; /* = p(1)'s in Chena experiment (upper site)*/
p(3)=0.0226     0.0226; /* = p(2)'s (middle site)*/
p(4)=0.0347567 0.0103797 /*p(3)'s (lower site), different for day and night groups*/
R(1)=82500      82500; /*N(1)'s for day and night groups*/
PROC STOP;

```

heterogeneity due to a timing effect in the last occasion (“ $p(4) = 0.0347567 \ 0.0103797$ ”).

In the program output all capture histories have an extra “1” in front of them representing the imaginary release occasion, which is ignored (outputted “1011” actually represents “011”). Capture histories for groups (subpopulations) were pooled before entering in Program Jolly.

Appendix 4: 1997 Survival Estimates

The survival estimates were:

Model A: $\hat{\phi}_1 = 1.25$, SE = 0.26, CI: 0.73 - 1.76; and

Model A': $\hat{\phi}_1 = 1.48$, SE = 0.27, CI: 0.95 - 2.01 .

The point estimates were both greater than 1.00, although precision was low and the confidence intervals contained 1.0. Survival estimators, unlike those for abundance, are based on marked animals only (Appendix 1), and may therefore have relatively low precision when capture probabilities are low.

The Deaths Only survival estimator, unlike the Model A estimator (see Appendix 1), compares two consecutive population estimates (Pollock et al 1990):

$$\hat{\phi}_i = \frac{\hat{N}_{i+1}}{\hat{N}_i - n_i + R_i} .$$

The high Deaths Only survival estimate was therefore a consequence of $\hat{N}_2 > \hat{N}_1$. The ratio $\hat{N}_2 / \hat{N}_1 = 199,302 / 133,468 = 1.49$, is close to the maximum likelihood output above.

The estimate \hat{N}_2 was may have been biased and caused the estimate $\hat{\phi}_1$ to likewise be poor.

Appendix 5: Chum Salmon Mark Recapture

A Lincoln-Petersen abundance estimate was attempted for chum salmon. Chum were marked with an upper partial caudal fin clip at the upper site, ignored at the middle site, and inspected for marks at the lower site. Although two lower site personnel had worked on the Chena project previously and were adept at checking for marks, there were no recaptures. The number of upper site releases was 573, and the number of lower site unmarked captures was 865. Captures by location and date are listed in Appendix 2.

The lack of recaptures resulted either from marks being overlooked or from induced, delayed mortality of marked fish. As noted in previous seasons (Peterson 1997), caudal clips on chum smolts are very difficult to see because the fish are small and have clear fins (unlike chinook). Average length was 37 mm (SE = 3) in the 1996 season (Daigneault 1997). With respect to survival, fin-clipping is relatively more deleterious in smaller fish (Nielsen 1992). The 1996 chum salmon survival estimate was extremely low ($\phi = 0.135$, SE = 0.0476), probably due in part to the above causes (Peterson 1997).